Non-native seaweeds in the rocky intertidal zone in the Little Corona Del Mar Area of Special Biological Significance: Effects on native community structure and diversity and investigation into the feasibility of local eradication

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TABLE OF CONTENTS

SUMMARY

In the rocky intertidal ecosystem of the Area of Special Biological Significance at Little Corona del Mar (Robert Badham Park) in Newport Beach, California, USA and in other rocky intertidal locations in southern California, the non-native seaweeds *Sargassum muticum* and *Caulacanthus ustulatus* are major contributors to community structure and ecosystem primary productivity. Despite the presence of these seaweeds since 1999 for *Caulacanthus* and the 1970s for *Sargassum*, little is known about their impacts on native community structure or ecosystem functioning. The purpose of this study was to examine the impacts of these seaweeds on native assemblages through comparisons of tidepools or rock patches where the non-native seaweed was present and where it was absent. Additionally, the feasibility of locally eradicating these species was experimentally tested on a local scale (tidepool or small patch) by removing either *Sargassum* or *Caulacanthus* and comparing percent cover and recovery rates to unmanipulated pools or patches with and without the non-natives present.

The impacts of these non-native seaweeds on native communities are mixed. *Sargassum* had little impact on community assemblages in intertidal tidepools in Newport Beach despite causing marked changes in light penetration and buffering temperature changes during low tide. Other studies examining the impacts of *Sargassum muticum* on native communities, both along this coast and in Europe, exhibited similar patterns in some cases while being contradictory to other studies highlighting a variable impact geographically and across different ecosystems. *Caulacanthus* had a negative impact on macroinvertebrates and a positive impact on seaweeds and meiofauna in the upper intertidal zone; conversely, minimal impact of *Caulacanthus* was observed in the middle intertidal zone. Zonal differences in impacts are likely due to the novel turf that *Caulacanthus* provides in the upper intertidal zone, where native seaweeds are uncommon in the region. This turf affords a microhabitat where sand accumulates and moisture is retained that provides refuge for seaweeds and meiofauna that normally would not be found in that habitat. In the middle intertidal zone, a native turf already exists, thus the presence of *Caulacanthus*, which often grows intertwined in the native turf, does not alter normal community structure. This study highlights that impacts can be different depending on the native taxa of concern and can vary among non-native seaweeds and within the same non-native species over different geographic regions or among different microhabitats within a location.

Eradication of these species required a high effort and was destructive to native flora and fauna. In removal plots, local eradication efforts proved unsuccessful as the non-native seaweeds recovered to levels equal to that of non-manipulated plots. The manipulations of herbivores in combination with removal also proved unsuccessful for both non-native seaweeds. The combination of minimal impacts on native species, the high effort required for removal, and quick recovery suggest that efforts to eradicate these species are not worthy of consideration.

Products of research as of January 2014:

Manuscript under review:

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Presentations:

Smith, J.R., S.C. Vogt, F. Creedon, B. Lucas, and D. Eernisse. Tidal zone variation in the effects of the non-native red alga *Caulacanthus ustulatus* on native rocky intertidal communities. Western Society of Naturalists Meeting, Ventura, CA. November 2013.

Smith, J.R. Rocky intertidal restoration. . Urban Ecology meeting, Newport Beach, CA. May 2013.

LIST OF FIGURES

LIST OF TABLES

Table 11. ANOSIM results (Global R and p- value) of community assemblage comparisons. Included are results from the Two-Factor ANOSIM (Patch and zone as fixed factors) as well as the ANOSIM results for the individual tidal zones.

Table 12. SIMPER results for species contributing most to dissimilarity between native and non-native patches in the upper and middle intertidal zones for cover, macroalgal presence, macroinvertebrate counts, and macro/meiofauna abundances.

Table 13. Mean abiotic, seaweed, and macroinvertebrate cover (+/-SE) in native and non-native plots at the end of the year-long study. Designation of plots as being native or non-native were established at the beginning of the study but, by the end of the study, these designations were no longer strong descriptors as *Caulacanthus* cover varied among plots. T-Test p-values are reported for each zone separately.

Table 14. Mean abiotic, seaweed, and macroinvertebrate cover (+/-SE) in treatments plots (Non-*Caulacanthus* Control, *Caulacanthus* Control, and *Caulacanthus* Removal) at the end of the year-long study. ANOVA p-values are reported for each zone separately.

Table 15. Mean macroinvertebrate counts (+/-SE) in native and non-native plots at the end of the year-long study. Designation of plots as being native or non-native were established at the beginning of the study but, by the end of the study, these designations were no longer strong descriptors as *Caulacanthus* cover varied among plots. T-Test p-values are reported for each zone separately.

Table 16. Mean macroinvertebrate count (+/-SE) in treatments plots (Non-*Caulacanthus* Control, *Caulacanthus* Control, and *Caulacanthus* Removal) at the end of the year-long study. ANOVA p-values are reported for each zone separately.

Table 17. ANOSIM results comparing community structure using both cover data and macroinvertebrate abundances. Two-Factor ANOSIM compare zones and either patches (native vs non-native) or treatments. Also included are ANOSIM results for the upper and middle intertidal zone separately for patches and treatments.

Table 18. SIMPER results for species contributing most to dissimilarity between native and non-native patches in the upper and middle intertidal zones for both cover and macroinvertebrate count data sets.

Table 19 SIMPER results for species contributing most to dissimilarity between pairwise comparisons of the three treatments in the upper and middle intertidal zones for both cover and macroinvertebrate count data sets.

1. INTRODUCTION

The introduction and subsequent invasion of non-native species is among the greatest threats to biodiversity and native ecosystem functioning (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Mack et al. 2000). Through the effects of competition, predation, and habitat alteration, biological invasions can reduce native species abundances (Race 1982; Delibes et al. 2004; Carlsson and Lacoursiere 2005) and diversity (Casas et al. 2004; Wikstrom and Kautsky 2004), alter community structure (Posey 1988; Stimpson et al. 2001; Britton-Simmons 2004), result in evolutionary consequences (Daehler and Strong 1997; Grosholz 2002), and modify ecosystem functioning, such as microbial dynamics, productivity, and nutrient cycling (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Hahn 2003).

Much work has been conducted on the effects of non-native species in terrestrial systems, but the abundance, distribution, and ecological effects of non-indigenous marine species in coastal systems is understudied (Grosholz 2002). The unbalanced study of terrestrial ecosystem invasions is evidenced by the fact that more than 90 % of approximately $1 billion spent on non-native species in the United States was allocated to the U.S. Department of Agriculture with less than 1 % of this spending aimed towards aquatic invaders (USCOP 2004). Further lacking in our understanding of invasions in marine systems is the study of non-native species of seaweeds. A recent global review (Williams and Smith 2007) of the distribution and impacts of non-indigenous species of seaweeds reveal that, of 407 global introductions, the ecological impacts of non-native seaweeds has been studied for only a small portion (6%). For the most part, a majority of these studies have concentrated on those species that have had multiple introductions worldwide and that have resulted in drastic community changes, such as with the invasive green alga *Caulerpa taxifolia* and the brown alga *Undaria pinnatifida*.

Recently, increased emphasis has been placed on the effect of non-native species on biodiversity and ecosystem functioning. For example, there is now a large literature base in terrestrial systems on the impacts of non-indigenous species on food webs and consumer/prey interactions, including work on the predation of native species by invaders (Fritts and Rodda 1998; Letnic et al. 2009) and on native herbivore interactions with non-native foods (e.g. Maron and Vila 2001; Agrawal and Kotanen 2003; Levin et al. 2004; Morrison and Hay 2011). Studies examining interactions between herbivores and exotic plants (e.g. Keane and Crawley 2002;

Wolfe 2002) have provided mixed results making it difficult to develop models with predictive value. In marine systems, only a few studies have been conducted with marine herbivores and non-native species of seaweeds, and these general exhibited mixed results (Scheibling and Anthony 2001; Stimson et al. 2001; Levin et al. 2002; Trowbridge 2002; Britton-Simmons 2004; Thornber et al. 2004; Sumi and Scheibling 2005; Valentine and Johnson 2005; Gollan and Wright 2006; Montiero et al. 2009; Vogt 2010).

Community level changes (biodiversity and community structure) resulting from the presence of exotic species have also been heavily studied in terrestrial systems (see Pimentel et al. 2005; Pysek and Richardson 2010) as well as in marine systems (see Bax et al 2003; Molnar et al 2008). However, the community level impacts of non-native species of seaweeds still constitute a major research gap. Observational and mensurative studies of community level impacts are most common with fewer experimental studies available. The impacts of non-native seaweeds on community structure are mixed with numerous examples of negative impacts on certain species or species groups. For example, the presence of *Caulerpa taxifolia* in the Mediterranean Sea has resulted in decreased abundances of seagrasses (Williams and Grosholz 2002). Alternatively, the presence of introduced seaweeds can result in no changes (Trowbridge 2001) or, in some cases, positive changes (Dumay et al. 2002) on certain species. These impacts, however, are complex and include numerous indirect effects that can be difficult to study. For example, *Sargassum muticum* in Washington can indirectly affect the abundance of sea urchins through shading of native kelps, the food source of urchins (Britton-Simmons 2004). Furthermore, although an invasive seaweed may be unpalatable or not used as a food source by native herbivores, the presence of the invasive can support a high abundance of epiphytes that can act as a food source for consumers (Williams and Smith 2007).

In addition to understanding the ecological consequences of non-native species, there is a great interest in understanding the potential ability to eradicate or control the spread of non-native species. Again, there is an unequal effort in terrestrial systems over marine systems with little research conducted on control of exotic seaweeds. For seaweeds, eradication or control is likely a difficult process due to the ability of seaweeds to grow and reproduce rapidly, to regrow from vegetative fragments, to have microscopic reproductive states that are difficult to detect, and to control the spread of spores in an open ocean system. Despite these difficulties in controlling non-native seaweed introductions, several examples of eradication efforts exist.

In urban southern California, coastal communities are being altered by the combined impacts of urbanization, climate change, and human visitation, a complexity of events that pose severe challenges to coastal managers. Previous research has revealed ecologically significant changes in the distributions and abundances of invertebrate and seaweed populations over the last 25 years, particularly on rocky shores near to urban centers. This includes changes in the number and abundance of non-native seaweeds (Bullard 2005; Whiteside unpubl. Data; Smith pers. obs).

Introductions of seaweeds in the southern California region have occurred repeatedly over the past few decades (Murray et al. 2006) and include, among others, the brown algae *Sargassum muticum*, *Sargassum horneri*, and *Undaria pinnatifida*, the green alga *Caulerpa taxifolia*, and the red algae *Caulacanthus ustulatus* and *Lomentaria hakodatensis*. Although some of these invasive seaweeds have been present for a long period of time, few investigational studies have been conducted on the biology or ecology of these species, particularly within the context of the southern California environment. The focus of this study is on two non-native seaweeds, *Sargassum muticum* and *Caulacanthus ustulatus*.

The non-native brown alga *Sargassum muticum* (Figure 1; Phaeophyceae, Fucales), native to SE Asia, is found in numerous regions worldwide, including multiple locations throughout Europe (Critchley et al 1983; Harries et al. 2007). It was introduced to the west coast of North America as early as 1902 (at least 1940s), probably as a consequence of importation of Pacific Oysters from Japan (Druehl 1973; Scagel 1956). This species quickly spread along the Pacific Coast, probably through local transport from fouling on boats, and was established in southern California intertidal habitats in the 1970s (Britton-Simmons 2004). This species is a major component of most southern California rocky intertidal and shallow subtidal locations. In rocky intertidal habitats, it can dominate tidepool habitats, taking up primary spaces as well as creating a canopy that may impact understory species or the abiotic conditions of the tidepools.

Sargassum muticum is a pseudo-perennial that has annual blades and a perennial discoid holdfast. The blades typically senesce in summer and early fall with the holdfast and portions of the thalli remaining in winter; the remaining unbladed thalli give it a wire appearance thus is known commonly known as wireweed. Seasonality has been shown to vary depending on temperature and geographic location (Thomsen et al. 2006; Harries et al. 2007a). The alga is monoecious with both male and female gametes produced on the same individual. It can reproduce asexually or sexually, including self-fertilization. Sexual reproduction often occurs while the zygote is attached to the parent plant with a developing germling being released and settling within 2-3 m of the adult (Deysher and Norton 1982). Longer distance dispersal can occur via floating fragments supported by buoyant pneumatocysts, which can remain viable and release germlings while in the water column (Deysher and Norton 1982; Critchley et al. 1983). Once settled, the species grows rapidly, between 2-4 cm per day (Jephson and Gray 1977; Critchley 1981; Lewey and Farnham 1981) and can reach lengths of up to 10 m in the subtidal zone, although greatly reduced in the intertidal zone.

Sargassum muticum has a large range of temperature and salinity tolerance. Maximal growth occurs at 25 °C, but can tolerate temperatures between 10-30 °C, and can survive through short periods of temperature well below 10 °C (Norton 1977; Nicholson et al. 1981; Hales and Fletcher 1989). The algae can also thrive in salinities from 24-34 ppt (Norton 1977, Hales and Fletcher 1989, Steen 2004), thus can be found in brackish waters, but its optimal salinity is that of normal seawater at ~34 ppt (Norton 1977; Hales and Fletcher 1989).

Sargassum muticum has many characteristics that make it a successful invader, including high growth rates, rapid colonization of space, high photosynthetic rates, copious reproduction including asexual and self-fertilization strategies, high temperature and salinity tolerances, high habitat complexity, and multiple dispersal mechanisms, including through drifting fertile thalli (Norton 1976; Critchley 1983; Rueness 1989; Viejo 1997).

Caulacanthus ustulatus (Figure 2) is a low-lying, turf forming red algae (Gigartinales, Rhodophyta) with long stolons and short, erect, and irregular branches with pointed apices. This species is found worldwide in warm temperate and sub-tropical waters and is considered an introduced species in multiple locations around the world, including California. On the eastern Pacific coastline, some disjunct historical records of the species can be found in British Columbia, Washington and Baja California; however, no records of the species in southern California were reported until 1999 (Bullard and Murray 2003) despite intense cataloguing of seaweed flora in the region since the 1950s. In southern California, *Caulacanthus* is found in upper and mid-shore rocky intertidal habitats and has been observed to overgrow numerous species, including barnacles, rockweeds, and mussels. *Caulacanthus* is common on many shores south of the Palos Verdes Peninsula to San Diego and on the warm Channel Islands (Anacapa and Santa Catalina); it can also be sporadically found up to San Francisco Bay but it rare north to British Columbia.

Little is known about the ecology, reproduction, and life history of *Caulacanthus*, especially in California. This species has a tri-phasic life history, like many Rhodophytes, alternating between spermatangial, tetrasporangial, and carposporophyte development. In southern California, previous work has found that most specimens are vegetative with only a small portion being tetrasporophytes; no carposporophytes were found (Whiteside unpublished data). This species is known to spread through vegetative fragmentation whereby broken pieces can re-attach to the substrate and grow into new individuals. *Caulacanthus* has been shown to have a wide range of temperature tolerances, with optimal growth occurring at ~23 °C (Choi and Nam 2005).

In the Little Corona del Mar (Robert Badham Park) Area of Special Biological Significance, the non-native brown alga *Sargassum muticum* and the non-native red alga *Caulacanthus ustulatus* are significant components of the habitat. Despite their obvious presence at this site and in the region, the role that these seaweeds have on community structure and biodiversity, as well as ecosystem functioning, has been previously understudied. The purpose of this project was to experimentally investigate the effects of both *Sargassum* and *Caulacanthus* on rocky intertidal community structure through comparisons of tidepools or patches where the non-native seaweed is absent and where it is present. Community structure was assessed by examining the abundances of seaweeds and invertebrates using cover and count sampling methods. Potential eradication was also experimentally examined by removing non-native seaweeds and monitoring recovery over time. In addition, the role that herbivores have in controlling the recovery of non-native seaweeds was also examined.

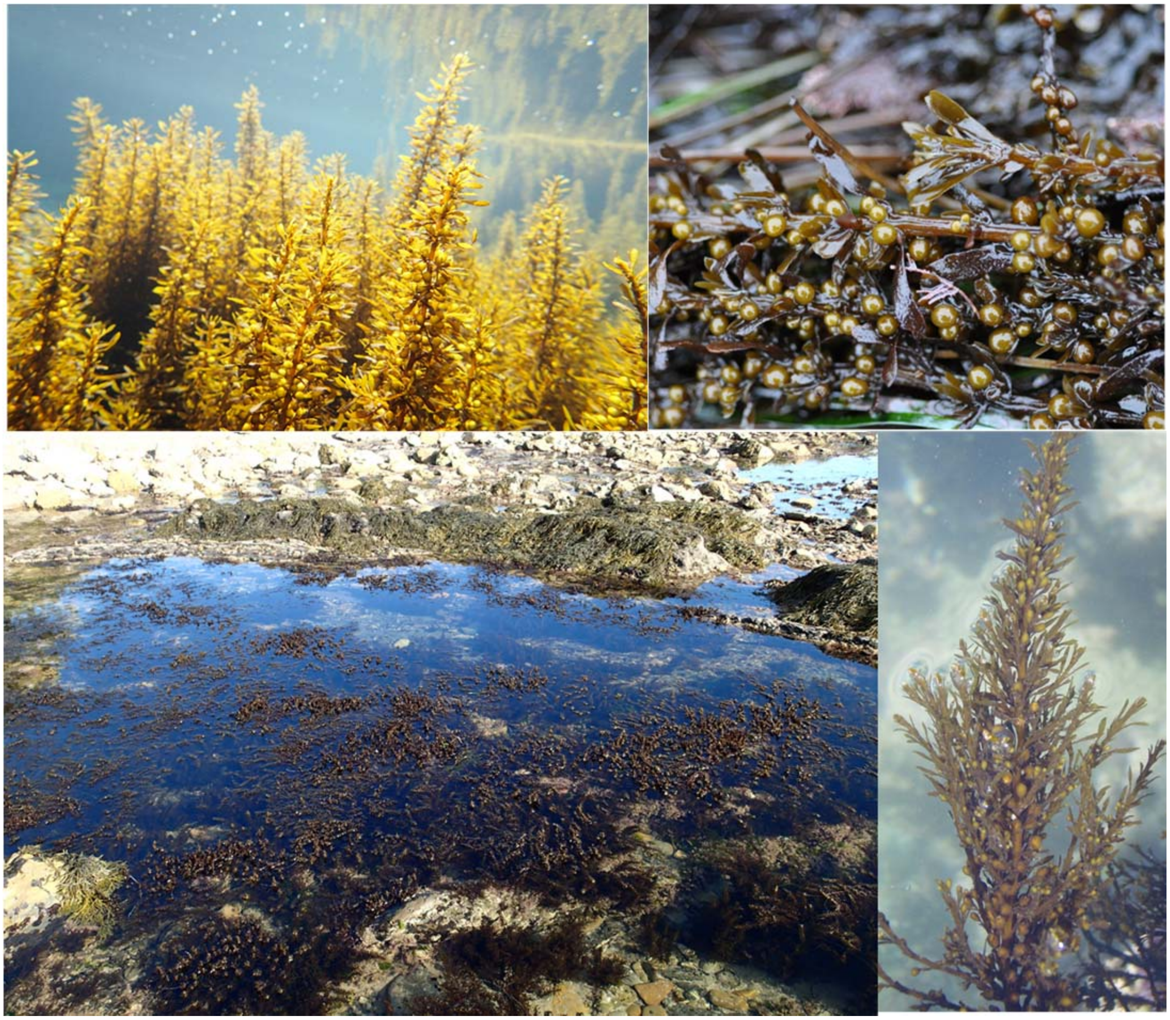

Figure 1. *Sargassum muticum* is a brown alga (Phaeophyceae; Fucales) that dominates intertidal and subtidal habitats. In the intertidal zone, this alga is typically found in tidepools in the upper, middle, and lower intertidal zones.

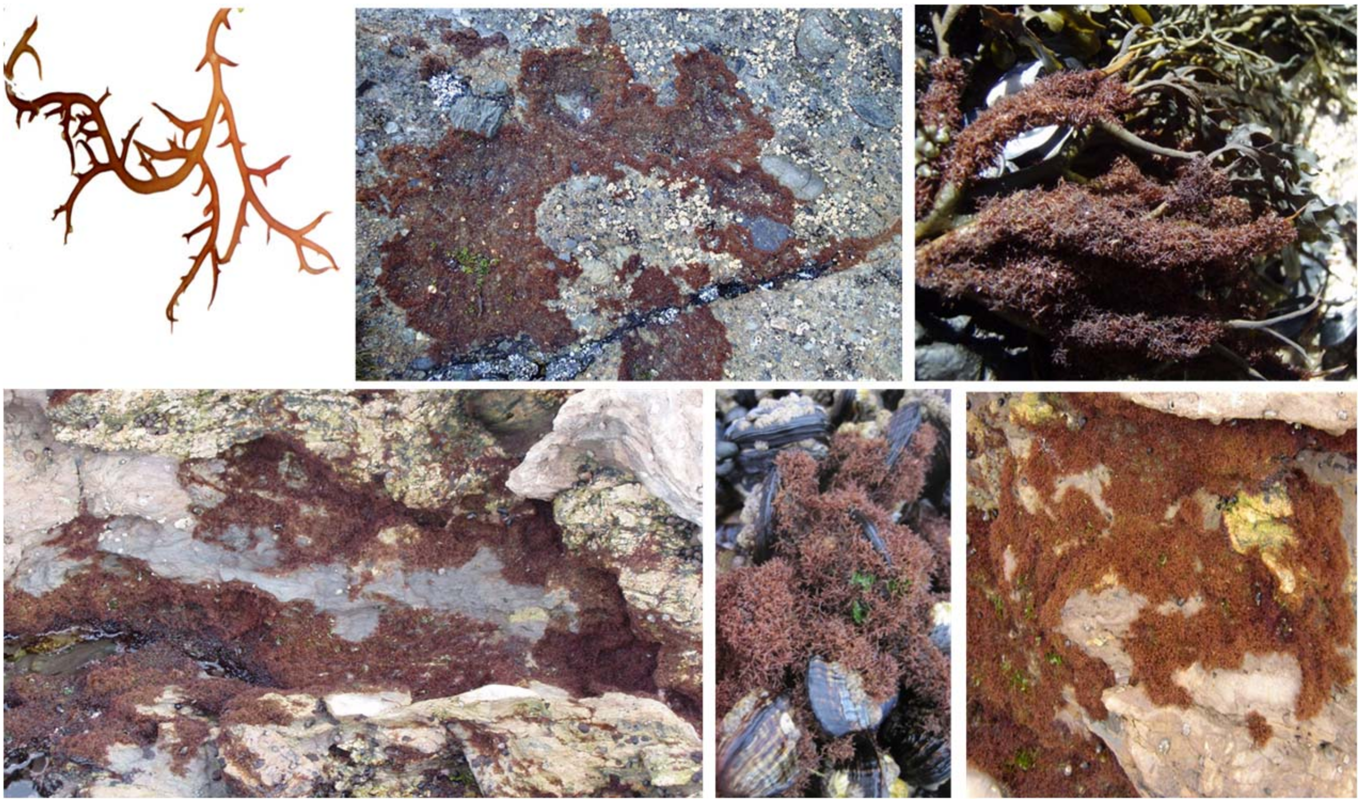

Figure 2. *Caulacanthus ustulatus* (Rhodophyta; Gigartinales) is a small turf forming red alga that can be found throughout the rocky intertidal ecosystem, particularly in the upper intertidal zone. In the middle intertidal zone, it can be found growing within native algal turfs, on rockweeds, and on mussels.

2. METHODS

2.0 Site Selection

This study was performed along a ~0.25 km rocky intertidal habitat extending from Little Corona del Mar and downcoast to Morning Canyon (Figure 3). The sampled habitat is bordered upcoast by Buck Gully and downcoast by Morning Canyon creek, both with persistent runoff from inland sources. Human visitation is significant in the upcoast portions of Little Corona del Mar and is reduced towards the downcoast portions into Morning Canyon.

Figure 3. Map of sampling locations along the coast of Newport Beach, CA from Little Corona del Mar to Morning Canyon. *Sargassum* pools and plots were distributed throughout the study site while *Caulacanthus* plots were focused within Little Corona del Mar.

2.1. ***Sargassum muticum***

2.11. Impacts on community structure.

To examine the impacts of *Sargassum* on native flora and fauna within rocky intertidal tidepools, 28 small to moderately sized pools (~0.4-3.1 m^2) were selected along a shoreline from Little Corona del Mar to Morning Canyon in February 2012. Smaller sized tidepools were chosen to reduce size effects and because there were a limited number of large pools from which to choose. To account for possible variations in location and tidal height, seven sets of four tidepools were chosen relatively close in location and estimated to be at similar tidal levels (0.44 – 4.8 ft.; within block variation of <1 ft.). Within each block, one pool contained no *Sargassum* (native pools) while 3 non-native pools had *Sargassum* (total n=7 and 21); three *Sargassum* pools were chosen for establishment of experimental removal treatments (see section 2.13). Given the variable size in tidepools (0.42-3.1 m^2), a 0.35 m^2 plot was established within the pools and permanently marked for temporal monitoring. Percent cover of *Sargassum* was determined using a modified point contact method whereby *Sargassum* located beneath a grid of 100 uniformly distributed points was determined and percent cover calculated. The initial cover of *Sargassum* pools mostly ranged between ~59% to 100% *Sargassum* canopy cover, with exception of two plots with a low cover of 29% and 40%. The average for all non-native pools was 82.3% *Sargassum* cover.

The percent cover of macroscopic flora and fauna attached to the substrate below the *Sargassum* canopy was assessed and the number of macroinvertebrates within plots counted. Percent cover was determined visually using a modified point contact method whereby bare rock, sand, and species, or higher level taxa when appropriate, were determined underneath the 100 points on gridded plots. Based on the number of hits out of a possible 100 points, percent cover was calculated. In cases where layering occurred, all species were accounted for, sometimes resulting in more than 100% cover within a plot. In addition to percent cover, all macroinvertebrates were also counted. The cover of *Sargassum* was ignored in community composition assessment as the goal was to determine the impact of *Sargassum* on species composition.

Percent cover data of all taxa (ignoring *Sargassum* cover) and the number of macroinvertebrates was analyzed by using both univariate statistics on individual taxa data and multivariate statistics on community structure. For each taxa, an ANOVA was used to determine differences between plots with and without *Sargassum* with *Sargassum* presence as a fixed factor and block as a random factor. For percent cover data, taxa were then combined based on functional groups for macrophytes (Littler and Littler 1980) and feeding guilds for macroinvertebrates and analyzed using an ANOVA (*Sargassum* presence fixed factor, blocks random factor). Diversity (species richness and Pielou's evenness) was calculated for each data set and analyzed using a similar randomized block ANOVA. For community structure analysis, cover data was square root transformed while macroinvertebrate counts were log transformed; for both data sets, a Bray Curtis Similarity matrix was calculated. A multidimensional scaling plot (MDS) was produced which plots samples on a two dimensional graph with plots with similar community composition located closer to each other. A Two Factor Analysis of Similarities (ANOSIM; *Sargassum* presence and block nested in *Sargassum* presence) was used to determine significance difference in community structure between pools with and without *Sargassum* for both data sets. A Similarities Percentage Test (SIMPER) was used to determine the species contributing most to this dissimilarity.

2.12. Impacts on abiotic conditions.

Dissolved oxygen (mg/L), salinity, and pH were measured in plots with and without *Sargassum* on two days in February 2012 using a YSI Professional Probe System. Tidepool dissolved oxygen, salinity, and pH were measured initially during a low tide period and remeasured between 1.5-2.5 hours later with data converted to change in parameters per hour period. Measurements over time were replicated 39 times in *Sargassum* pools and 13 times in non-*Sargassum* pools. Data sets were analyzed using a t-test to determine differences in native and non-native pools. During this same sampling period, light intensity loss was measured using Quantum Spherical Light Sensor by measuring light intensity (lum/ft) in the air and in the water either underneath *Sargassum* canopies (n=45) or in pools without *Sargassum* (n=15). The percent aerial light intensity loss was calculated per replicate and compared between pool types using a t-test.

Light and Temperature Loggers (HOBO Pendant, Onset) were placed into tidepools with and without *Sargassum* canopy (Figure 4; n=3 each), as well as on the cliff to get aerial temperature and light (n=1), on two occasions, April 4-5 and November 4-5, 2013, to examine ~day long trends. Loggers were fixed to 10 pound dive weights to ensure that they remained upright during high tides. In April 2013, measurements were made every minute for ~17 hours while in November 2013, measurements were made every 10 second for ~16 hours. In April, low tide was in the late morning through early afternoon while low tide was during the late afternoon into evening in November. The same tidepools were not used during both sampling periods. The average temperature and light intensity was calculated for both sets of pools and compared to aerial conditions. In addition, the difference in temperature and light intensity between non-*Sargassum* pools and *Sargassum* pools within blocks, adjusting for differences in tidal height of paired pools. For light, the percentage of light lost compared to aerial light intensity was determined.

2.13. Removal effort and success.

Following initial community structure determination in February 2012 (Methods 2.11), tidepools within each of 7 block were assigned a treatment consisting of: a) No *Sargassum* control, b) *Sargassum* control, c) *Sargassum* removal, and d) *Sargassum* removal with seagrass (*Phyllospadix torreyi*) transplants (n=7 for each treatment). Due to the failure of seagrass to survive transplanting, many of these plots were more similar to *Sargassum* removal treatments. Initial *Sargassum* cover was significantly different among treatments because of the non-*Sargassum* controls (ANOVA; Treatment df=3, F=39.9, p<0.001; Block (random) df=6, F=1.43, p=0.258) but the *Sargassum* plots themselves were significantly similar (Tukey's multiple comparisons test – see Figure 20). Analyzing the plots with *Sargassum* treatments alone, without non-*Sargassum* plots, supports this assumption (ANOVA; Treatment df=2, F=0.66, p=0.536; Block (random) df=6, F=1.51, p=0.526) as well as revealing that *Sargassum* cover was similar among blocks (ANOVA; df=6, F=1.58, p=0.233).

For removal treatments, all *Sargassum* holdfasts within 0.35 m^2 plots were scraped off the rock (Figure 5), attempting to remove all portions of the holdfast. The biomass removed within plots was collected and the wet weight determined. In addition, the time to remove *Sargassum* from plots was also recorded. Following clearing of the plots, *Sargassum* was also cleared from the rest of the tidepool, weighed, and effort determined as with application of plot treatments. For seagrass transplants, thin pieces of rock with the seagrass *Phyllospadix torreyi* attached were chipped off the substrate from surrounding areas, ensuring that the roots of the seagrass remained strongly attached to the rock piece (Figure 5). The rock pieces(s) were then epoxied to the substrate within appropriate plots and pools using Z spar marine epoxy; this epoxy is used frequently to attach equipment to the substrate in the rocky intertidal zone and does not affect the health of marine organisms. For No *Sargassum* and *Sargassum* control replicates, nothing was manipulated. Removal plots were revisisted every two weeks for 6 weeks to remove any *Sargassum* that was missed or that started to regrow from missed pieces of holdfasts. This was done to attempt to ensure that the initial removal treatment was complete.

Starting in April 2012, plots were revisited every two months until February 2013 to assess *Sargassum* canopy cover, using the point contact method described previously. On occasion, the *Sargassum* canopy cover was conducted on a monthly basis.

Community structure of all other taxa was determined every two months until February 2013, using percent cover assessments and counts of macroinvertebrates as initially conducted in plots prior to application of treatments (Methods 2.11). Only the final community structure after the year-long study was analyzed.

Percent cover of *Sargassum* over time was analyzed using a Repeated Measures ANOVA with treatment and time as fixed factors and plot nested in treatment as a random factor (blocks could not be analyzed in this model). The cover of *Sargassum* at the end of the experiment was analyzed using an ANOVA with treatment as a fixed factor and block as a random factor. For community structure analysis for the final data set at the end of the year-long study, cover data was square root transformed while macroinvertebrate counts were log transformed; for both data sets, a Bray Curtis Similarity matrix calculated. A Two Factor Analysis of Similarities (ANOSIM; Treatment and Block) was used to determine significance difference in community structure among treatments for each sampling period; additional comparisons were made of native plots (no *Sargassum* control) and non-native plots (all other treatments).

2.14. Phlorotannin concentrations.

Many brown seaweeds (Phaeophyceae) contain phlorotannins that are used to deter herbivory. It is believed that the genus *Sargassum* typically has relatively high levels of phlorotannins thus reducing the impacts of grazing by herbivores. To examine phlorotannins in *Sargassum,* a Folin-Ciocalteau procedure was used. *Sargassum muticum* samples were collected in the high, mid, and low intertidal zones at Little Corona Del Mar to compare variations among tidal zones. To determine congeneric differences in phlorotannin concentrations, samples of *S. muticum, S. agardhianum, S. horneri,* and *S. palmeri* were collected from Catalina Island where all four species coexist in the same shallow subtidal habitat. *S. agardhianum* and *S. palmeri* are both native to southern California while *S. horneri* is another non-native species found in this region.

To determine the dry weight to wet weight relationship, 0.100 – 0.150 g of tissue was removed from 10 individuals of each species or from each tidal level. The samples were weighed to the nearest 0.001 g and placed in a drying oven at 60 ^{o}C for 48 hr. After 48 hr, the samples were re-weighed to the nearest 0.001 g. To determine the relationship between the dry and wet weight, the following equation was used: Dry Weight/Wet Weight. The ratio was then used to calculate the dry weight of each sample used in the phlorotannin extraction process since only the wet weight of the sample could not be determined from analyzed samples.

Approximately 0.100 – 0.145 g of tissue from 10 individuals from each tidal height or of each species was measured for phlorotannin extractions. In a glass beaker surrounded by ice, algal tissue was added to 15 ml of 80% Methanol. The algal material and methanol were homogenized together for 4-5 min using a 20 mm Omni Homogenizer. The homogenized material was transferred to a 50 ml centrifuge tube and placed in a refrigerator for 24 hr for extraction.

After 24 hr, the homogenates were centrifuged at 3000 RPM for 6 min. In a separate 50 ml centrifuge tube, 50 µl of centrifuged homogenate was mixed with 1 ml of DI water and 1 ml of 40% Folin-Ciocalteau Working Reagent. One ml of 2 N Na_2CO_3 solution was added to the mixture and heated to 50^{o}C for 30 min.

A spectrophotometer was used, first calibrated using a blank that was prepared by mixing 50 µl of 80% methanol, 1 ml of DI water and 1 ml of 40% Folin-Ciocalteau Working Reagent in a 50 ml centrifuge tube. After 5 min, 1 ml of 2 N Na_2CO_3 solution was added to the mixture. The mixture was then heated to 50^oC for 30 minutes in a drying oven. Cuvettes with sample solutions were placed in a spectrophotometer and the absorbance measured at 765 nm. A total of 10 individuals per tidal height or 10 individuals per species were used in the experiment.

To calculate the phlorotannin concentration of each sample, a standard curve was prepared using phloroglucinol. A mixture of 0.20 g of phloroglucinol and 200 ml of DI water was prepared and diluted to create solutions with the following concentrations: 0.05, 0.01, 0.005, 0.001, 0.0005, 0.0025, 0.00125, and 0.0075 g phloroglucinol/100 ml. The relationship between the absorbance and phloroglucinol concentration was calculated to determine the standard curve: y=4.21x + 0.004. This allowed the phlorotannin g/ml of each algal sample to be calculated and the phlorotannin concentration determined using the following equation:

$$\text{Phlorotannin Concentration} = \frac{\text{phlorotannin g / ml X 15 ml of methanol}}{\text{Dry Weight of Algal Sample}} \text{ x } 100$$

2.15. Impacts of herbivorous urchins.

Observationally, tidepools that were dominated by urchins appeared to have lower cover of *Sargassum*. To test this observation, 98 pools were haphazardly sampled from Little Corona del Mar to Morning Canyon in June 2012. The percent cover of *Sargassum*, the number of *Sargassum* holdfasts (approximate since individuals are difficult to distinguish when holdfasts are clumped together), and the number of urchins in pools were determined. A relationship between cover or holdfast number with urchin number was determined.

In February 2013, 20 small to moderately sized (0.6-3.1 m^2) tidepools with *Sargassum* present were established from Little Corona del Mar to Morning Canyon. Pools were divided into blocks, based on similar location and estimated tidal height, with four pools within each block. Permanent plots (0.35 m^2) were established within the tidepools for long-term monitoring. Plots were then assigned one of four treatments in a two factorial design: control, *Sargassum* removal, urchin transplant, and *Sargassum* removal + urchin transplant. Initial cover in plots ranged from 60-100%, except two plots that initially were lower in cover (>25%). Initial cover varied significantly among treatments (ANOVA, Treatment df=3, F=4.26, p=0.029; Block df=4, F=7.78, p=0.002) with the urchin plots having a higher initial cover than controls but with all other plots being equal.

As previously described, *Sargassum* was removed by scraping off all *Sargassum* holdfasts from the entire tidepool and removing the biomass (Figure 6). For urchin transplants, 45-75 urchins, depending on the size of the tidepool, were removed from surrounding non-experimental pools and placed into appropriate treatment tidepools, distributed evenly around the pool and within the plot (Figure 6). Since it was expected that urchins would emigrate out of the tidepools, a high number were transplanted with expectations that a proportion would remain. Urchins already located in tidepools, including controls, were not manipulated to reduce confounding factors.

The percent cover and holdfast number (approximate) of *Sargassum* were monitored in plots on a monthly basis through December 2013 (10 months), as was the percent cover of *Sargassum* in the entire tidepool and the density of urchins in the pool. Plot cover, pool cover, and holdfast number were analyzed using a Repeated Measures ANCOVA with urchin transplant (yes or no), removal (yes or no), and time as fixed factors, plot nested within treatment as a random factor, and urchin number as a covariate. Data sets were also analyzed at the end of the ~10 month using an ANOVA with urchin transplant and removal as fixed factors and blocks as a random factor.

2.16. Large tidepool preliminary investigations.

At Little Corona del Mar, a large pool (~250 m^2) contained a high abundance of *Sargassum muticum*. This high intertidal pool was used to determine whether there is a relationship between *Sargassum* and the entrapment and accumulation of sand, a possible side effect of *Sargassum* presence. The relationship between sand and *Sargassum* was only tested in the large tidepool as, observationally, this did not occur in small to moderately sized pools; thus, this is a characterization of a one microhabitat. To examine the relationship between sand and *Sargassum*, 0.35 m^2 plots were randomly located in the large pools and the percent cover and holdfast number (approximate) of *Sargassum* and cover of sand were determined using the point contact method previously described. In April 2012, 59 plots were assessed while 64 plots were assessed in November 2012 to determine temporal differences.

In addition, an examination of the effort and success of removal of *Sargassum* on a larger scale was conducted in the large tidepool. This was done to determine if the recovery rate in large pool with patches of *Sargassum* remaining in it would differ from smaller-sized experimental tidepools where all *Sargassum* was removed. To examine effort and success of removal in the large pool, 14 one m^2 plots were randomly located within the pool and all *Sargassum* removed within plots as previously described (Figure 7). Sargassum in portions of the large of the large tidepool were not removed. The number of holdfasts removed and the effort, in person hours to accomplish this, was determined. *Sargassum* recovery was to be monitored over time but was aborted as during a revisit 2 months following removal, plots that were scraped clean were visually similar to adjacent non-scraped areas. Due to the quick recovery, monitoring was not conducted.

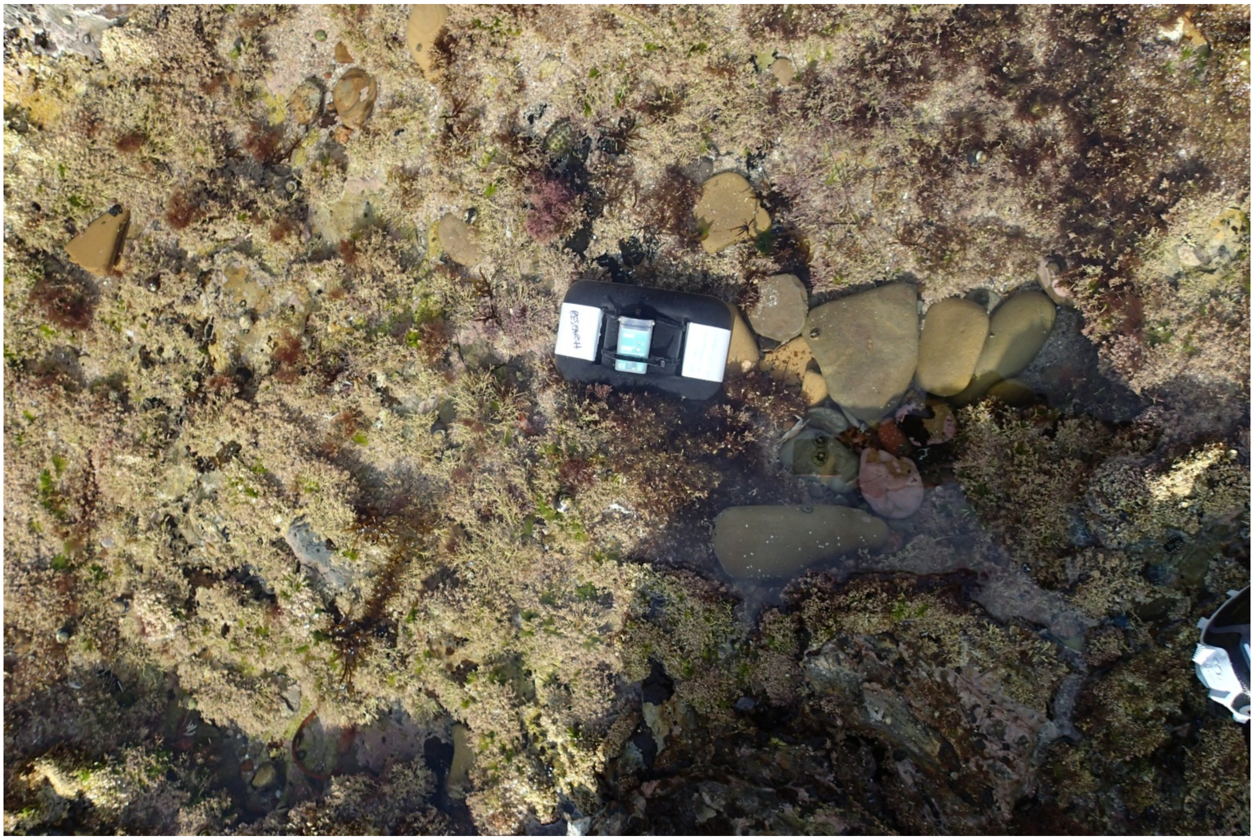

Figure 4. Light and temperature loggers (Onset; HOBO) placed in tidepools without *Sargassum* (above) and in tidepools underneath the *Sargassum* canopy (not pictured).

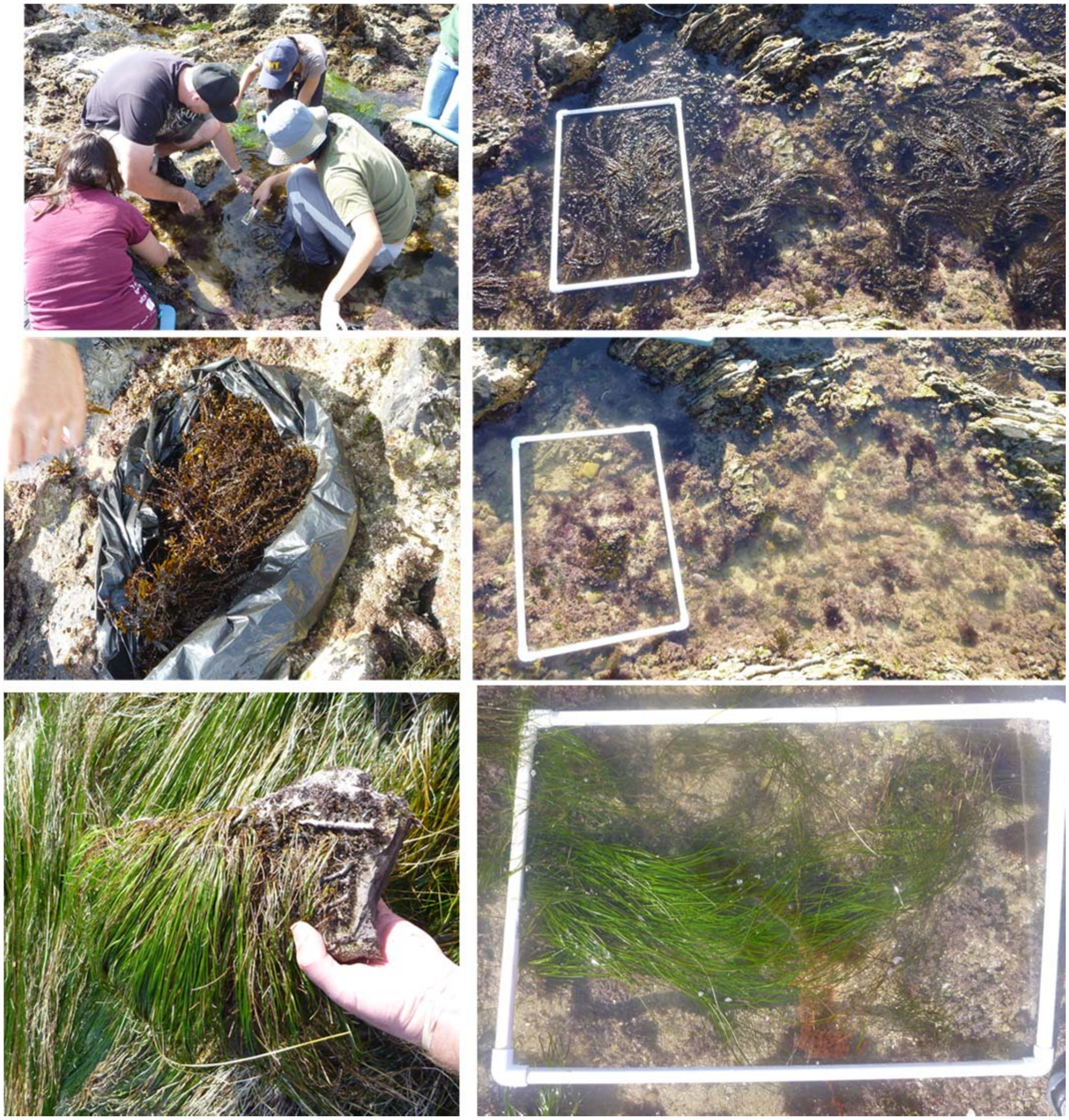

Figure 5. The process of removing *Sargassum muticum* from pools and transplanting of the surfgrass *Phyllospadix torreyi*.

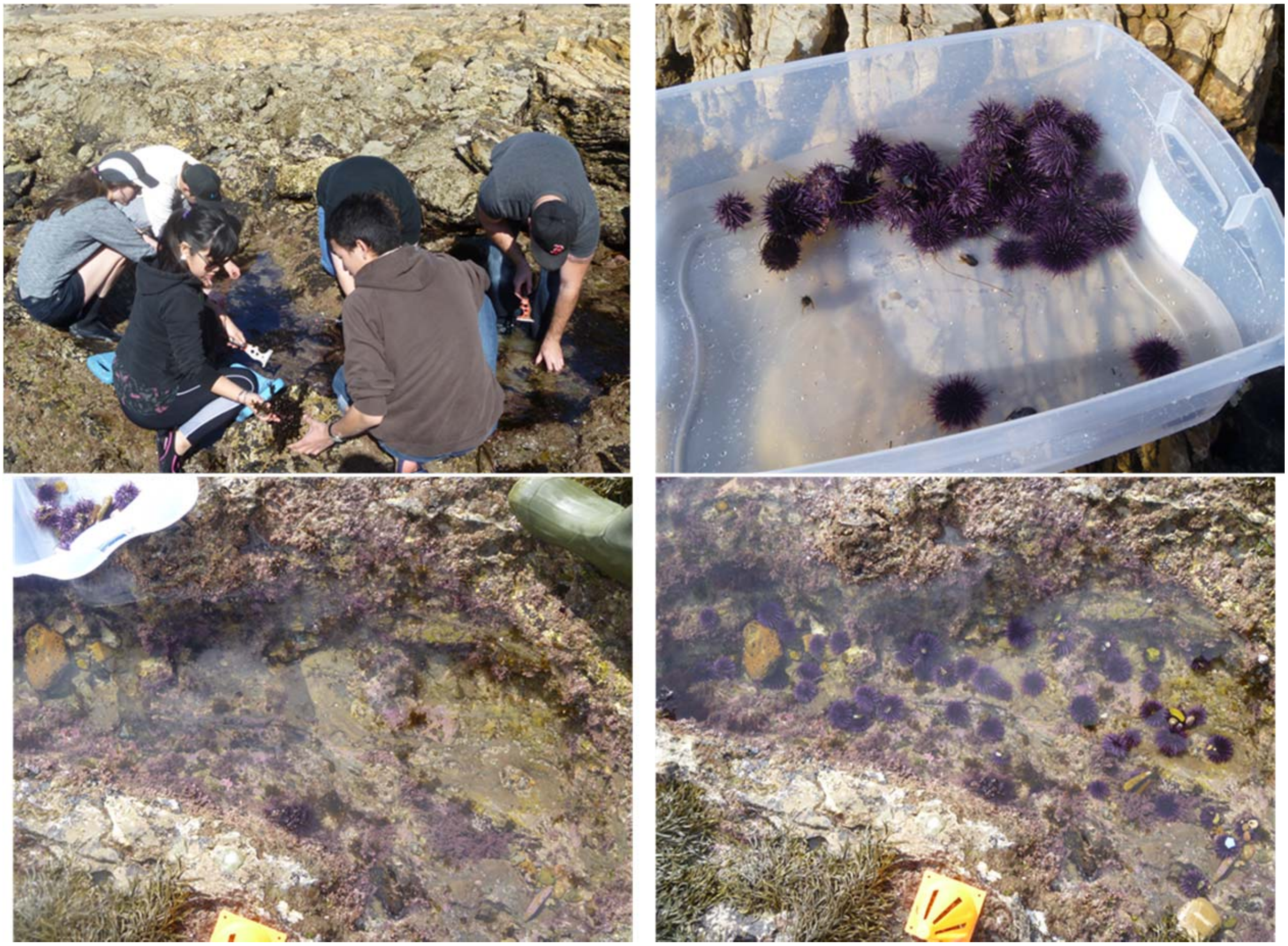

Figure 6. Removal of *Sargassum muticum* and transplanting of urchins.

Figure 7. Removal of *Sargassum muticum* in the big tidepools.

<u>**2.2. *Caulacanthus ustulatus***</u>

2.21. Impacts on community structure.

To examine the impacts of *Caulacanthus* on native flora and fauna, 33 plots (400 cm^2) were established in Little Corona del Mar. Eighteen plots were established within the middle intertidal zone with 6 plots having low to no cover of *Caulacanthus* (<10% but typically 0%) and 12 plots containing at least ~35% *Caulacanthus*; extra *Caulacanthus* plots were established for experimental removal experiments (see section 2.22). In the high intertidal zone, 5 plots without *Caulacanthus* and 10 plots with *Caulacanthus* were established. In the high zone, native plots were characterized by bare rock and high intertidal species, such as barnacles, limpets, and periwinkles. In the middle intertidal zone, native plots were characterized by native red algal turfs consisting of various filamentous like species and articulated corallines. In non-native plots in the middle intertidal zone, *Caulacanthus* was growing mixed in with native algal turfs. Percent cover of *Caulacanthus* was determined visually and ranged between 35-85%.

The community composition of native and non-native assemblages was determined using four data sets. First, cover of rock, sand, and all taxa were determined visually within plots. Second, the percent cover of all macrophytes were transformed into presence/absence data. Third, all macroinvertebrates visible to the naked eye were counted within plots. Finally, subplots (13.7 cm^2) were sampled to examine all invertebrate species, particularly targeting the meiofaunal assemblages living within algal turfs but with macroinvertebrates also quantified. To do this, core samples within algal turfs were collected, taken to the laboratory, and all invertebrates identified at higher taxonomic levels (typically class or order) under a dissecting scope (to 10X) and counted. In the high zone, turf samples were collected within plots for those assigned as a removal treatment (see section 2.22). In order to not affect the percent cover of *Caulacanthus* in non-native plots that served as *Caulacanthus* control plots in subsequent experiments, core samples were taken from *Caulacanthus* turfs located adjacent to established plots. In high intertidal native plots, no turf was available for collection and consisted mostly of bare rock, limpets, and barnacles. Therefore, subplot invertebrate counts were conducted in the field using field scopes (to 10X). In the middle intertidal zone, core samples were taken within plots for those replicates assigned the *Caulacanthus* removal treatment while core samples were taken just outside established plots for remaining plots. In the middle intertidal zone, a native turf is present thus core samples were made. In addition to quantifying invertebrates within all core samples, the amount of sediment was also measured; no sediment was detectable in upper intertidal native plots.

The four data sets, all cover, macroalgal presence, and macrofauna abundance in large plots and macro- and meiofauna abundances in subplots, were compared using univariate and multivariate techniques. Each taxa was compared among native plots without *Caulacanthus* and non-native plots with *Caulacanthus* in each zone separately using a T-test. Species richness and diversity (H') was calculated for all data sets (except H' for macroalgal presence) and compared among zones using a T-Test.

In testing for the effect of *Caulacanthus* on macroalgae community assemblages, the presence of *Caulacanthus* was excluded from the multivariate analyses (for the cover data set and the macroalgal presence data set). A resemblance matrix was calculated for each data set using a Bray-Curtis similarity which was then used to create multi-dimensional scaling (MDS) plots. A two factor Analysis of Similarities (ANOSIM) was used to determine significant differences in community structure between zones and between native and non-native patches for each data set. In addition, ANOSIM analyses were conducted on the zones individually. A Similarities Percentage (SIMPER) test was used to determine which species are contributing most to dissimilarities between patches for each zone separately.

2.22. Removal effort and success.

The established plots within the high and middle intertidal zone were assigned one of three conditions in February 2012. Plots without *Caulacanthus* served as native controls while plots with *Caulacanthus* were assigned as either *Caulacanthus* control plots, which were unmanipulated, or *Caulacanthus* removal plots where plots were first scraped using putty knives to removal all biota from the rock followed by burning of the substrate using a torch (Figure 8). *Caulacanthus* cover was similar between treatments prior to initiation of the experiment (T-test p=0.689; *Caulacanthus* control mean = 58.7 +/- 5.0; Removal mean = 61.4 +/-4.4), even if the zones are separated (T-test High zone p=0.907 [CC=63.0 +/-5.6, R=62.0 +/- 6.1]; mid zone p=.642 [CC=55.8 +/-7.7, R=60.8 +/- 7.0]). The percent cover of *Caulacanthus* was monitored on a ~bi-monthly basis until February 2013, as was the number of macroinvertebrates and the percent cover of all taxa visible to the naked eye; subplot core sampling for meiofauna was not resampled following the initial assessment. The community structure determined during the final sampling period at the end of the year-long study was analyzed; however, community structure data collecting during the experimental period were not analyzed.

The percent cover of *Caulacanthus* was examined over time using a Repeated Measures ANOVA with Treatment, Zone, Time, and Plots nested in Treatment as fixed factors and Plots as a random factor. Cover was then analyzed over time individually for the two intertidal zones using a Repeated Measures ANOVA with Treatment, Time, and Plots nested in Treatment as fixed factors and Plots as a random factor. The final percent cover at the end of the experiment was compared among treatments using an ANOVA with Treatment and Zone as fixed factors. Additional ANOVA analyses were conducted on the final cover separately for each zone (Treatment as a fixed factor).

2.23. Impacts of herbivorous limpets.

To examine the potential impact of herbivory on the recovery of *Caulacanthus* after removal, the upper intertidal limpet *Lottia scabra* was transplanted into experimental plots. *L. scabra* is known to be a generalist epilithic microfilm grazer (Sutherland 1972), however others (Branch 1981; Morelissen and Harley 2007) suggest it likely grazes any suitable material on the rock surface (i.e., very small to microscopic fragments or early crustal stages of macroalgae); it was used in this experiment because it was the most common, larger (approximately 2.5 cm maximum diameter at Little Corona del Mar) mobile invertebrate within the upper intertidal that had the potential to consume small to microscopic fragments of *Caulacanthus*.

Twenty one 400 cm^2 plots were established in the upper intertidal zone at Little Corona del Mar on February 10, 2013. Plots were randomly assigned as: 1) control plots, 2) removal plots, and 3) removal plots with the addition of *L. scabra*. For removal plots, all biota were removed as previously described (scraped and torched). In removal + transplant plots, 70 *L. scabra* with a maximum length of greater than 2 cm were collected onsite from tidal heights similar to the experimental plots and relocated to each of the R+T plots (10 limpets per plot).

Limpet relocation occurred during the first three sampling months to ensure that approximately 10 limpets were within each Treatment plot for the duration of the experiment. *L. scabra* abundances and percentage cover of *Caulacanthus* was sampled each month until November, 2013.

A Repeated Measures ANCOVA, with treatment and time as fixed factors, plots nested within treatments, plots as a random factor, and *L. scabra* abundance as a covariate, was used to test differences between the three plot-type trajectories over time. In addition, an ANOVA (treatment as a fixed factor) was used to test differences between the three plot types before manipulation (Pre-Treatment) and at the end of the 10-month experiment to detect if the relocation of limpets into cleared plots significantly aids in the control of *Caulacanthus*.

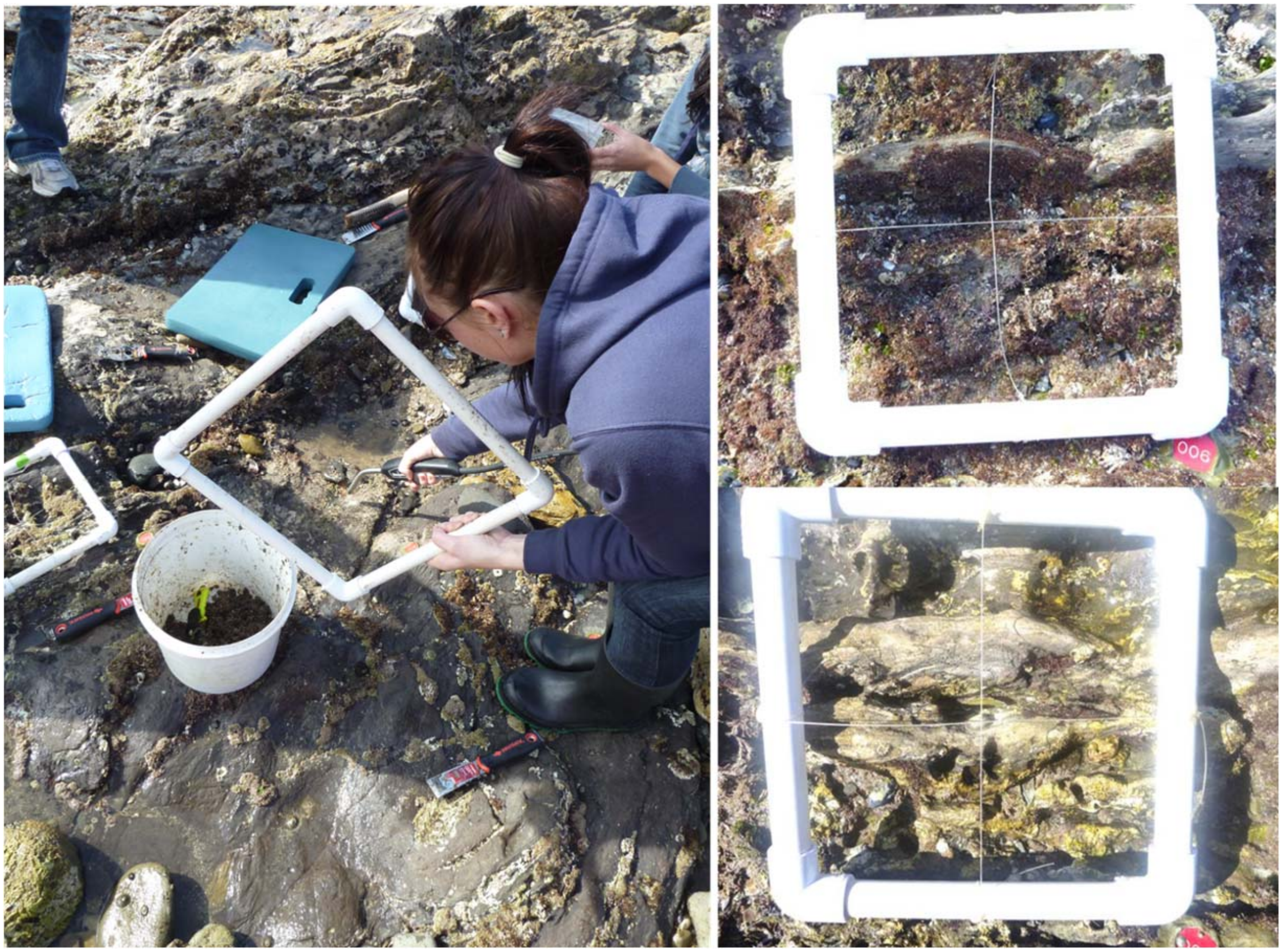

Figure 8. Scraping and torching of *Caulacanthus* plots.

3. RESULTS

3.1 *Sargassum muticum*

3.11. Impacts on community structure.

Comparisons of the percent cover of understory species in *Sargassum* pools and native pools yielded few differences for species and functional group/feeding guild using univariate analyses (Table 1, Randomized block ANOVA). As would be expected, the percent cover of *Sargassum* holdfasts was significantly higher in *Sargassum* pools. Two species, *Dictyota flabellata* and *Osmundea sinicola*, were higher in native pools as was the scavenger feeding guild. All remaining species, taxa, and functional groups/feeding guilds were significantly similar in *Sargassum* and native pools. For mobile invertebrates, univariate analyses revealed significant differences only for the limpet complex *Lottia scabra/conus* (Table 2, Randomized block ANOVA) which was found to be more abundant in the native plots without *Sargassum*. Species richness from cover data ranged from about 14-16 species while macroinvertebrate count richness was between ~4-5 species (Figure 9); Pielou's evenness for cover data was ~0.6 while ~0.94 for macroinvertebrate count data. No data set was significantly different between non-*Sargassum* and *Sargassum* plots; one block effect was significant for Pielou's evenness for cover data:

		Richness			Pielou's Evenness		
		df	F	p value	df	F	p value
Cover Data	*Sargassum* presence	1	0.41	0.528	1	0.94	0.345
	Block	6	0.93	0.496	6	4.17	**0.008**
Macroinvertebrate Counts	*Sargassum* presence	1	3.63	0.870	1	1.43	0.363
	Block	6	1.82	0.152	6	1.43	0.257

Multivariate analyses of cover data reveal that community structure was significantly similar in *Sargassum* pools and native pools (ANOSIM Global R=0.083; p=0.192; Figure 10); a significant block effect was observed (ANOSIM Global R=0.488; p=0.001). The species contributing most to the dissimilarity included a higher percentage of rock, encrusting brown algae, and *Lithothrix aspergillum* in *Sargassum* pools, and a higher cover of Crustose Corallines in native pools. As with percent cover data, there were no differences in community structure using mobile invertebrate counts between *Sargassum* pools and native pools (Figure 11; ANOSIM Global R=0.032; p=0.315); a significant block effect, however, was detected (ANOSIM Global R=0.261; p=0.009). The species contributing most to the dissimilarity included a higher percentage of the limpets *Lottia strigitella*, *Lottia limatula*, and *Lottia scabra/conus* as well as the hermit crab *Pagurus samuelis* and trochid snail *Agathostoma eiseni* in native pools.

Table 1. Mean percent cover (+/1 SE) of rock, sand, seaweed taxa, invertebrate taxa, and functional forms/feeding guilds in native plots without *Sargassum* and plots with the non-native *Sargassum* present. Also presented are p-values from the ANOVA (*Sargassum* presence as a fixed factor and block as a random factor).

					ANOVA pvalues	
	Native Pool Mean	**Native Pool SE**	***Sargassum* Pool Mean**	***Sargassum* Pool SE**	**Sargassum/No Sargassum (Fixed Factor)**	**Block (Random Factor)**
Abiotic						
Rock	15.3	5.0	16.8	3.3	0.794	**0.049**
Sand	3.9	2.3	11.5	4.0	0.288	0.317
Seaweeds:						
Corallina pinnatifolia/vancouveriensis	36.8	5.4	26.6	3.5	0.125	0.193
Psuedolithoderma /Ralfsia	15.4	5.9	6.6	2.0	0.085	0.452
Lithothrix aspergillum	9.4	7.9	5.8	2.4	0.385	**0.001**
Crustose Coralline	5.3	2.4	11.7	3.5	0.179	**0.005**
Pterocladiella capillacea	3.9	2.3	4.8	1.4	0.674	**0.019**
Ulva californica	1.5	0.6	1.3	0.4	0.865	0.289
Dictyota coriaceum	1.2	0.8	3.0	1.2	0.355	0.090
Sargassum muticum holdfast	0.0	0.0	4.6	1.0	**0.017**	0.304
Hypnea valentiae	3.3	3.1	1.3	0.5	0.265	0.096
Ceramium spp.	2.0	1.8	0.5	0.3	0.165	0.093
Chondria achorizophora	0.1	0.1	0.2	0.1	0.853	0.183
Corallina chilensis	0.0	0.0	0.7	0.5	0.419	0.243
Lomentaria hakodotensis	1.6	1.1	0.7	0.3	0.225	0.434
Chondracanthus canaliculatus	1.0	0.7	1.5	0.6	0.624	0.051
Silvetia compressa	1.9	1.9	0.5	0.5	0.223	**0.030**
Acrosorium ciliolatum	0.0	0.0	1.2	0.6	0.198	0.125
Centrocera clavulatum	0.1	0.1	0.0	0.0	0.428	0.568
Cryptopleura crispa	2.2	2.2	0.6	0.3	0.194	0.148
Phyllospadix roots	0.0	0.0	0.1	0.1	0.576	0.472
Jania crassa	0.0	0.0	0.8	0.4	0.325	0.683
Caulacanthus ustulatus	0.9	0.9	0.0	0.0	0.108	0.436
Colpomenia sinuosa	0.1	0.1	0.1	0.1	0.576	0.667
Cladophora spp	0.0	0.0	0.2	0.1	0.428	0.119
Dictyota flabellata	0.9	0.6	0.1	0.1	**0.046**	0.584
Chaetomorpha linum	0.0	0.0	0.0	0.0	0.576	0.472
Osmundea sinicola	0.7	0.4	0.1	0.1	**0.039**	0.352
Dictypoterus undulata	0.0	0.0	0.1	0.1	0.428	0.568
Bossiella orbigniana	0.1	0.1	0.0	0.0	0.428	0.568
Laurencia pacifica	0.0	0.0	0.0	0.0	0.576	0.472
Hindebrandiacea	0.0	0.0	0.0	0.0	0.576	0.472

Table 1 continued

	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	ANOVA pvalues Sargassum/No Sargassum (Fixed Factor)	Block (Random Factor)
Invertebrates:						
Anthopleura sola/elegantissima	2.2	1.4	0.6	0.2	0.075	0.343
Strongylocentrotus purpuratus	2.4	2.1	0.8	0.4	0.269	0.261
Lottia limatula	0.5	0.1	0.2	0.1	0.053	0.868
Agathostoma eiseni	0.4	0.1	0.2	0.1	0.153	0.833
Pagurus spp.	0.4	0.1	1.2	0.8	0.554	0.285
Lottia strigitella	0.6	0.1	0.4	0.1	0.437	0.642
Mytilus californianus	0.3	0.2	0.2	0.2	0.925	0.264
Lottia scabra/conus	0.4	0.2	0.1	0.1	0.042	0.085
Sculpin	0.3	0.1	0.2	0.1	0.457	0.515
Pachygrapsus crassipes	0.4	0.3	0.1	0.1	0.085	**0.033**
Nuttalina spp.	0.2	0.1	0.1	0.0	0.107	**0.000**
Aplysia californica	0.0	0.0	0.4	0.2	0.243	**0.048**
Unidentified shrimp	0.1	0.1	0.1	0.0	0.779	0.467
Cyanoplax hartwegii	0.1	0.1	0.1	0.1	0.680	0.622
Chlorostoma aureotincta	0.1	0.1	0.2	0.1	0.591	0.460
Chlorostoma funebralis	0.1	0.1	0.0	0.0	0.329	**0.029**
Phragmatopoma californica	0.0	0.0	0.3	0.3	0.576	0.472
Fissurella volcano	0.1	0.1	0.1	0.0	1.000	0.329
Girella nigricans, juvenile	0.1	0.1	0.0	0.0	0.329	**0.029**
Octopus spp.	0.0	0.0	0.1	0.1	0.497	0.515
Spirorbis spp.	0.0	0.0	0.0	0.0	0.576	0.472
Acanthinucella spirata	0.0	0.0	0.1	0.1	0.452	0.547
Lottia gigantea	0.0	0.0	0.0	0.0	0.576	0.472
Conus californicus	0.0	0.0	0.0	0.0	0.576	0.472
Norrisia norrisi	0.0	0.0	0.0	0.0	0.576	0.472
Unidentified gastropod	0.0	0.0	0.0	0.0	0.576	0.472
Tetraclita rubescens	0.1	0.1	0.0	0.0	0.083	0.391
Lottia digitalis	0.0	0.0	0.0	0.0	0.576	0.472
Orange Sponge	0.0	0.0	0.0	0.0	0.576	0.472
Unidentified clam	0.0	0.0	0.0	0.0	0.576	0.472
Flatworm	0.0	0.0	0.0	0.0	0.576	0.472
Strongylocentrotus fransiscianus	0.1	0.1	0.0	0.0	0.083	0.391

Table 1 continued

	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	ANOVA pvalues Sargassum/No Sargassum (Fixed Factor)	Block (Random Factor)
Functional Groups:						
Abiotic	26.0	10.5	26.0	3.5	0.997	0.767
Sheet Algae	3.7	1.8	3.1	1.0	0.736	0.176
Articulate Corallines	38.1	8.5	36.6	5.0	0.859	0.072
Filamentous-like Algae	0.7	0.6	1.5	0.8	0.528	0.179
Encrusting Algae	12.6	5.9	21.1	4.4	0.128	**0.000**
Fleshy Algae	8.8	3.1	13.3	2.7	0.299	**0.029**
Seagrass	0.0	0.0	0.1	0.1	0.576	0.472
Tough and Leathery Algae	3.9	1.9	4.4	1.1	0.814	0.648
Herbivores	5.0	2.6	2.9	0.5	0.125	0.009
Scavengers	5.5	2.3	1.1	0.3	**0.003**	0.201
Filter Feeders	1.5	1.0	0.4	0.2	0.131	0.434
Predators	0.3	0.2	0.1	0.1	0.487	0.281
Fish	0.4	0.1	0.2	0.1	0.085	0.243

Table 2. Mean mobile invertebrate count (+/1 SE) in 0.35 m^2 plots in native plots without *Sargassum* and plots with the non-native *Sargassum* present. Also presented are p-values from the ANOVA (*Sargassum* presence as a fixed factor and block as a random factor).

					ANOVA p values	
	Native Pool Mean	**Native Pool SE**	***Sargassum* Pool Mean**	***Sargassum* Pool SE**	**Sargassum/No Sargassum (Fixed Factor)**	**Block (Random Factor)**
Agathostoma eiseni	4.14	1.70	1.57	0.75	0.137	0.625
Anthinucella spirata	0.00	0.00	0.10	0.07	0.428	0.568
Aplysia californica	0.00	0.00	0.19	0.09	0.214	0.286
Chlorostoma aureotincta	0.71	0.57	1.00	0.38	0.702	0.411
Chlorostoma funebralis	0.14	0.14	0.19	0.19	0.883	0.182
Conus californicus	0.00	0.00	0.10	0.10	0.576	0.472
Cyanoplax hartwegii	0.14	0.14	0.24	0.12	0.680	0.622
Fissurella volcano	0.14	0.14	0.14	0.08	1.000	0.329
Lottia digitalis	0.00	0.00	0.14	0.14	0.576	0.472
Lottia gigantea	0.00	0.00	0.05	0.05	0.576	0.472
Lottia limatula	4.71	1.92	1.57	0.71	0.069	0.440
Lottia scabra/conus	5.43	2.41	0.48	0.20	**0.001**	0.172
Lottia strigitella	15.57	6.47	5.24	2.36	0.083	0.629
Norrisia norrisi	0.00	0.00	0.05	0.05	0.576	0.472
Nuttalina spp.	0.57	0.43	0.62	0.36	0.903	**p<0.001**
Octopus	0.00	0.00	0.10	0.07	0.428	0.568
Girella nigricans	0.14	0.14	0.05	0.05	0.329	0.029
Pachygrapsus crassipes	0.43	0.30	0.24	0.10	0.384	0.134
Pagurus samuelis	6.14	4.68	5.33	2.48	0.873	0.391
Sculpin	0.57	0.30	0.38	0.13	0.518	0.651
Shrimp	0.14	0.14	0.24	0.12	0.680	0.622
Strongylocentrotus fransiscianus	0.14	0.14	0.00	0.00	0.083	0.391
Strongylocentrotus purpuratus	0.43	0.30	1.81	0.68	0.248	0.277

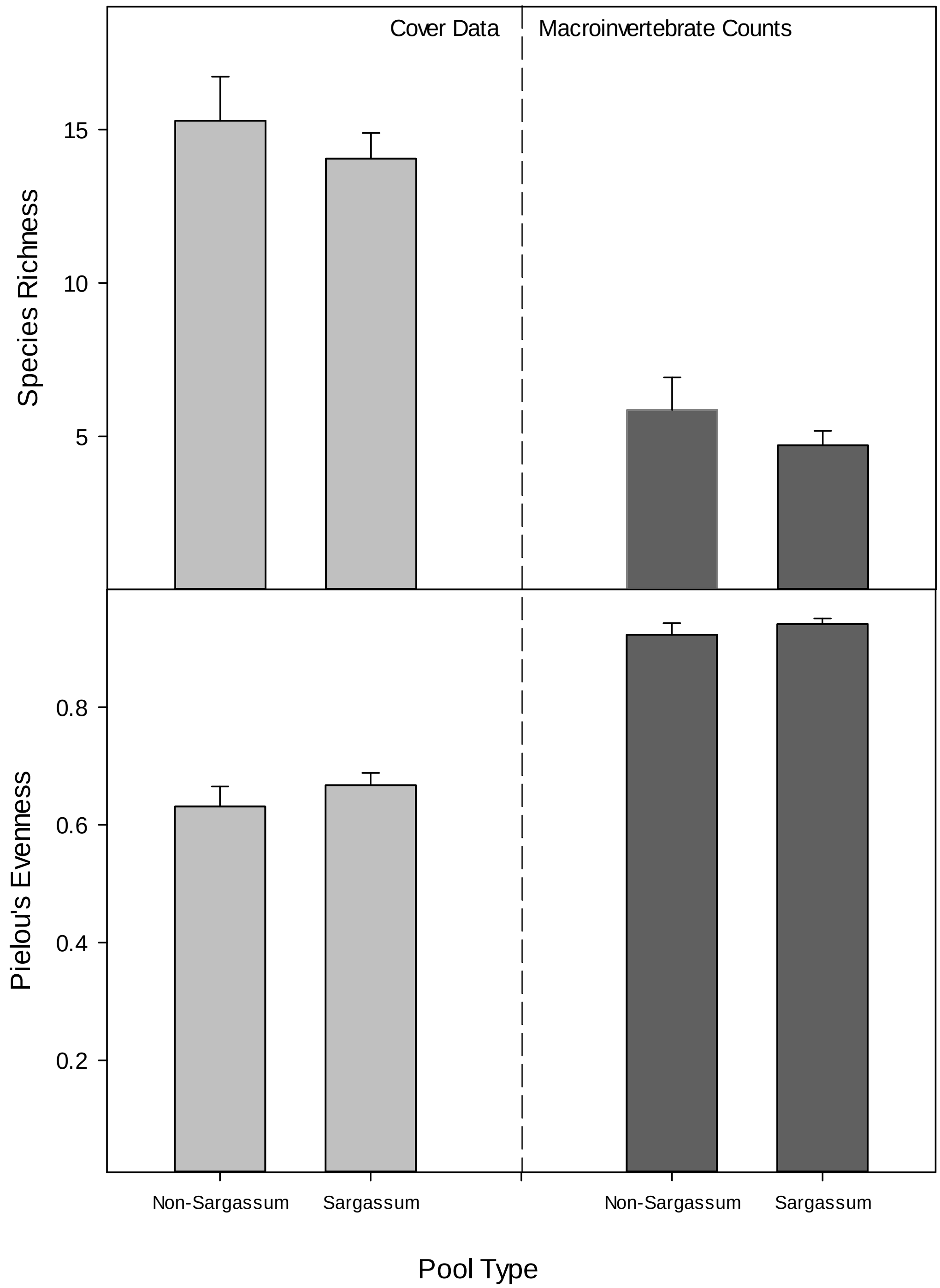

Figure 9. Mean species diversity (richness (upper figure) and Pielou’s Evenness (lower figure)) (+/- SE) for cover data (left) and macroinvertebrate counts (right). No significant difference was observed within any data set (ANOVA Treatment $p>0.05$; block $p>0.05$ except Pielou’s Evenness for Macroinvertebrate counts $p=0.008$).

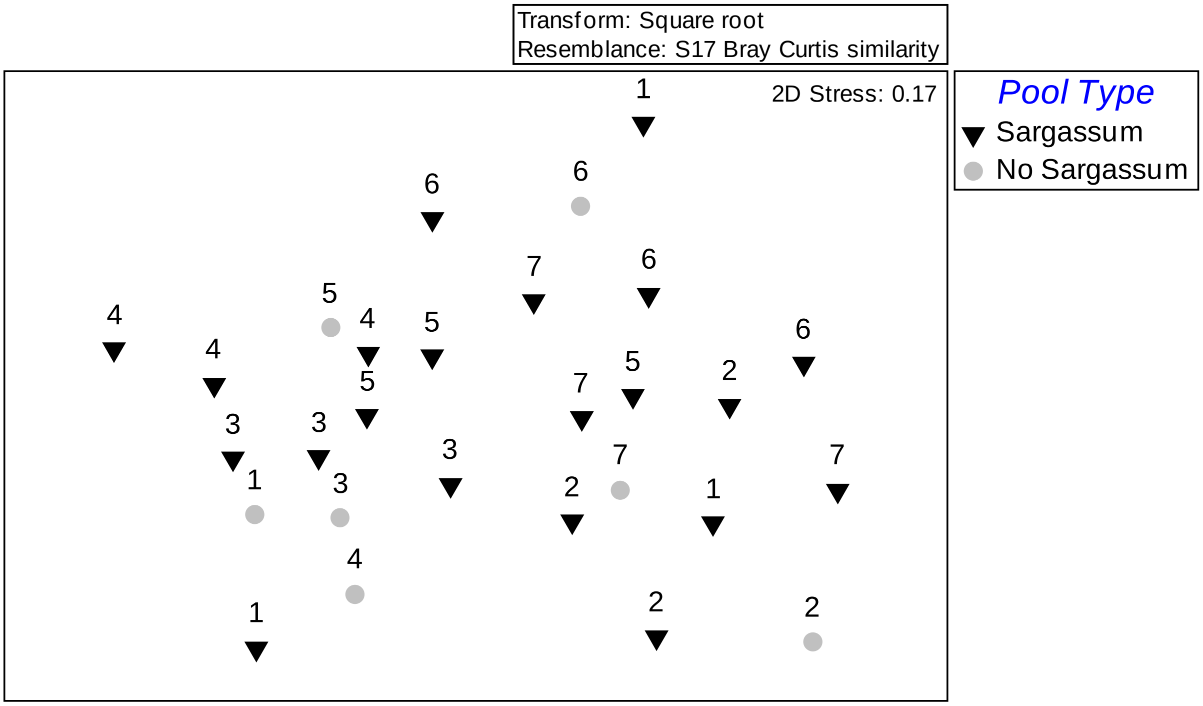

Figure 10. Multidimensional scaling plot of community structure using percent cover data in *Sargassum* pools and native pools without *Sargassum*. Block numbers are labelled. Community structure was similar between pool types (ANOSIM Global R=0.083; p=0.192); a significant block effect was observed (ANOSIM Global R=0.488; p=0.001).

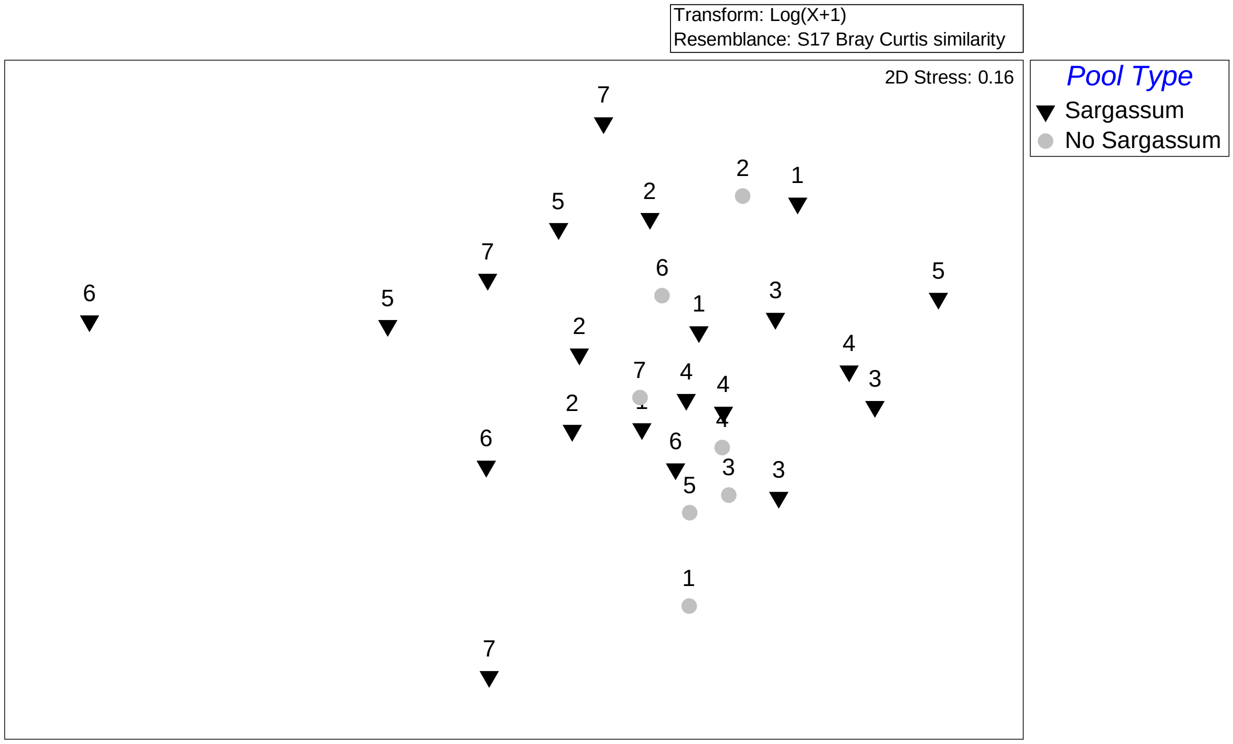

Figure 11. Multidimensional scaling plot of community structure using mobile invertebrate counts in *Sargassum* pools and native pools without *Sargassum*. Block numbers are labelled. Community structure was similar between pool types (ANOSIM Global R=0.032; p=0.315); a significant block effect was observed (ANOSIM Global R=0.261; p=0.009).

3.12. Impacts on abiotic conditions.

Hourly changes in dissolved oxygen (mg/L), pH, and salinity (ppt) in February 2012 did not vary significantly between tidepools with and without *Sargassum* (T-test $p>0.05$). The changes in dissolved oxygen per hour was highly variable among samples but neither plot types exhibited much of a change (non-*Sargassum* mean -0.63+/-0.41 SE; *Sargassum* mean 0.05+/-0.30 SE; T-test p=0.201). Similarly, pH only increased slightly in both pools (non-*Sargassum* mean 0.043+/-0.02 SE; *Sargassum* mean 0.071+/-0.02 SE; T-test p=0.299); salinity exhibited the same patterns (non-*Sargassum* mean 0.37+/-0.44 SE; *Sargassum* mean 0.0.21+/-0.16 SE; T-test p=0.733).

During daylight hours for the April 2013 sampling, air temperature reached a maximum of 54.3 °C while dropping down to 12.5 °C at night (Figure 12 upper). When submerged, both non-*Sargassum* and *Sargassum* tidepools remained steady at the sea temperature of 15.1 °C. However, during the late morning/early afternoon low tides, non-*Sargassum* pools were markedly warmer than *Sargassum* pools, reaching a maximum of 27.6 °C while *Sargassum* pools reached a maximum of 22.4 °C. The difference in temperature between non-*Sargassum* pools and *Sargassum* pools varied depending on tidal level (as indicated by blocks), with over a maximum 9 °C higher temperature in upper intertidal non-*Sargassum* pools (Figure 12 lower).

During daylight hours in November, aerial temperatures reached a maximum of 56.5 °C and a minimum of 8.8 °C at night (Figure 13 upper). While submerged, both pools stabilized at the sea temperature of 17.4 °C. Non-*Sargassum* pools heated up to a maximum of 23.9 °C during late afternoon low tides while *Sargassum* pools only reached a maximum of 20.6 °C. During a short low tide period at night when aerial temperature was lower than the ocean temperature (8.8 °C versus 17.4 °C), tidepool temperature was reduced, with the *Sargassum* pools (minimum 16.4 °C) cooling less than non-Sargassum pools (minimum 15.7 °C). The difference in temperature between non-*Sargassum* pools and *Sargassum* pools varied with blocks, with over a 4.7 °C higher temperature in upper intertidal non-*Sargassum* pools during day low tides (Figure 13 lower) and a -2 °C difference during the nighttime low tide.

The percent of aerial light intensity loss for periodic sampling over two low tide periods in February 2012 revealed that light loss was significantly higher in *Sargassum* pools (~97%)

than in non-*Sargassum* pools (~74%; Figure 14; T-test $p<0.001$). Light intensity was further investigated using light loggers that measured light every minute over a ~17 hour period in April 2013 and again in November 2013 over ~16 hour period with measurements recorded every 10 second. During April 2013 diurnal sampling, light intensity reached over 25,000 lum/ft during the day in the air but was greatly reduced underwater in tidepools (Figure 15 upper). In non-*Sargassum* pools, light intensity during the day mostly ranged around 8,000-12,000 lum/ft and was much higher than *Sargassum* pools which mostly maintained below light intensities of ~1,200 lum/ft. The difference in light intensity between non-*Sargassum* pools and *Sargassum* pools was approximately 8,000-12,000 lum/ft during the day time (Figure 15 lower). Furthermore, the percent of aerial light lost underneath *Sargassum* canopies ranged in the upper 90% while non-*Sargassum* tidepools exhibited an approximate 50-70% loss (Figure 16).

During November 2013 sampling, light intensity in the air reached a peak of almost 18,500 lum/ft during the day with a mid-day typical range between 12,000-17,000 (Figure 17 upper). Light intensity was greatly reduced in non-*Sargassum* pools with mid-day intensity ranging between 4-10,000 lum/ft. In *Sargassum* pools, light was further reduced, ranging around 500-2,000 lum/ft. The difference in light intensity was highly variable from morning through evening but was typically 3,000 to 12,000 lum/ft higher in the non-*Sargassum* pools (Figure 17 lower). In the mid-day November sampling, the percent of aerial light lost underneath the *Sargassum* canopy was greater than 95%. Markedly lower losses were recorded in non-*Sargassum* pools, although percent light losses were highly variable (Figure 18).

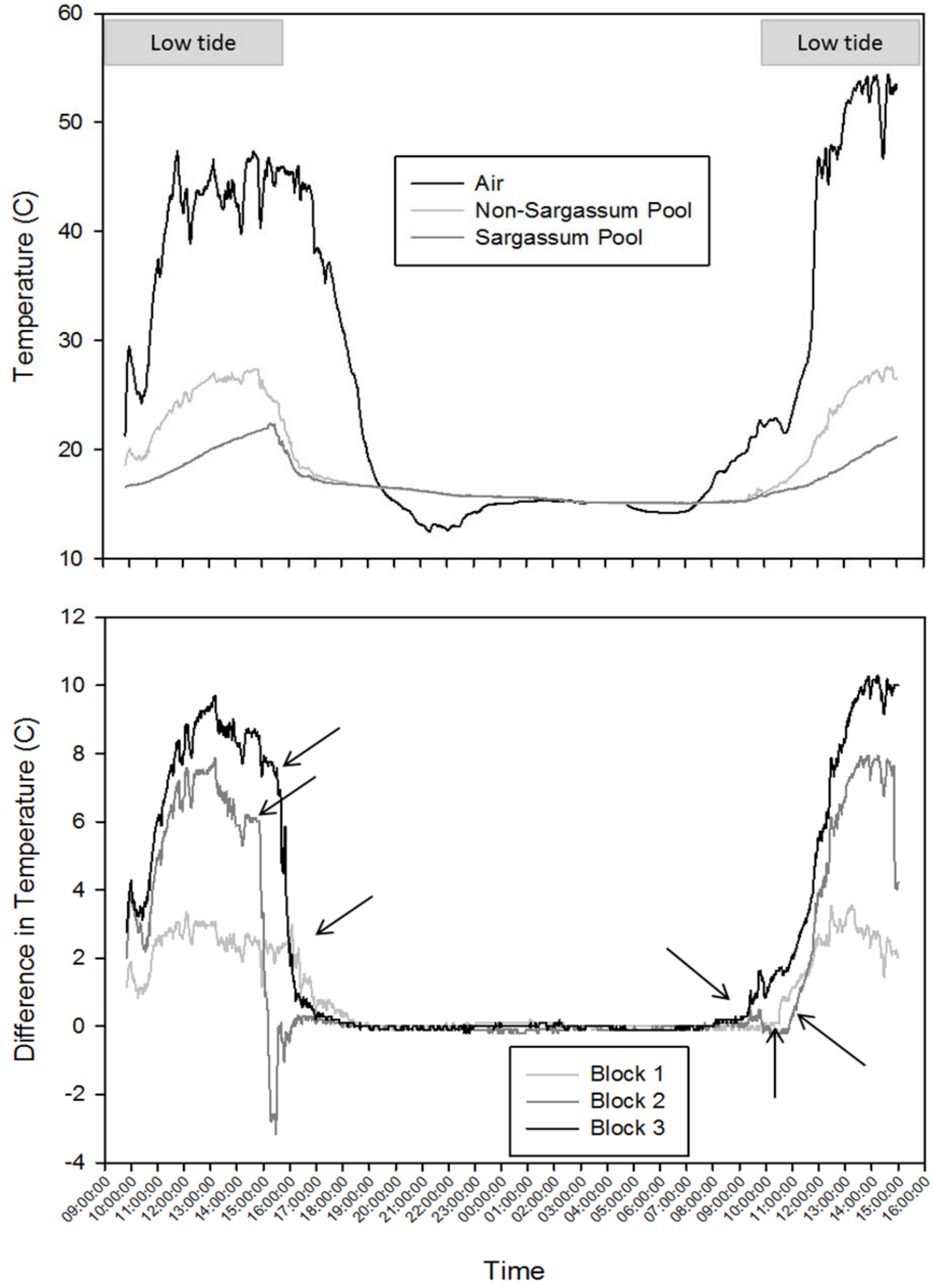

Figure 12. Mean temperature (°C) in air, in pools without *Sargassum*, and in pools with *Sargassum* in April 2013 is located in the upper figure. Indicated is the relative period of low tide when pools were no longer submerged. The difference in temperature (Non-*Sargassum* pools minus *Sargassum* pools) for paired blocks over time are located in the lower graph. The arrows indicate the approximate time at which the pools within blocks were no longer submerged.

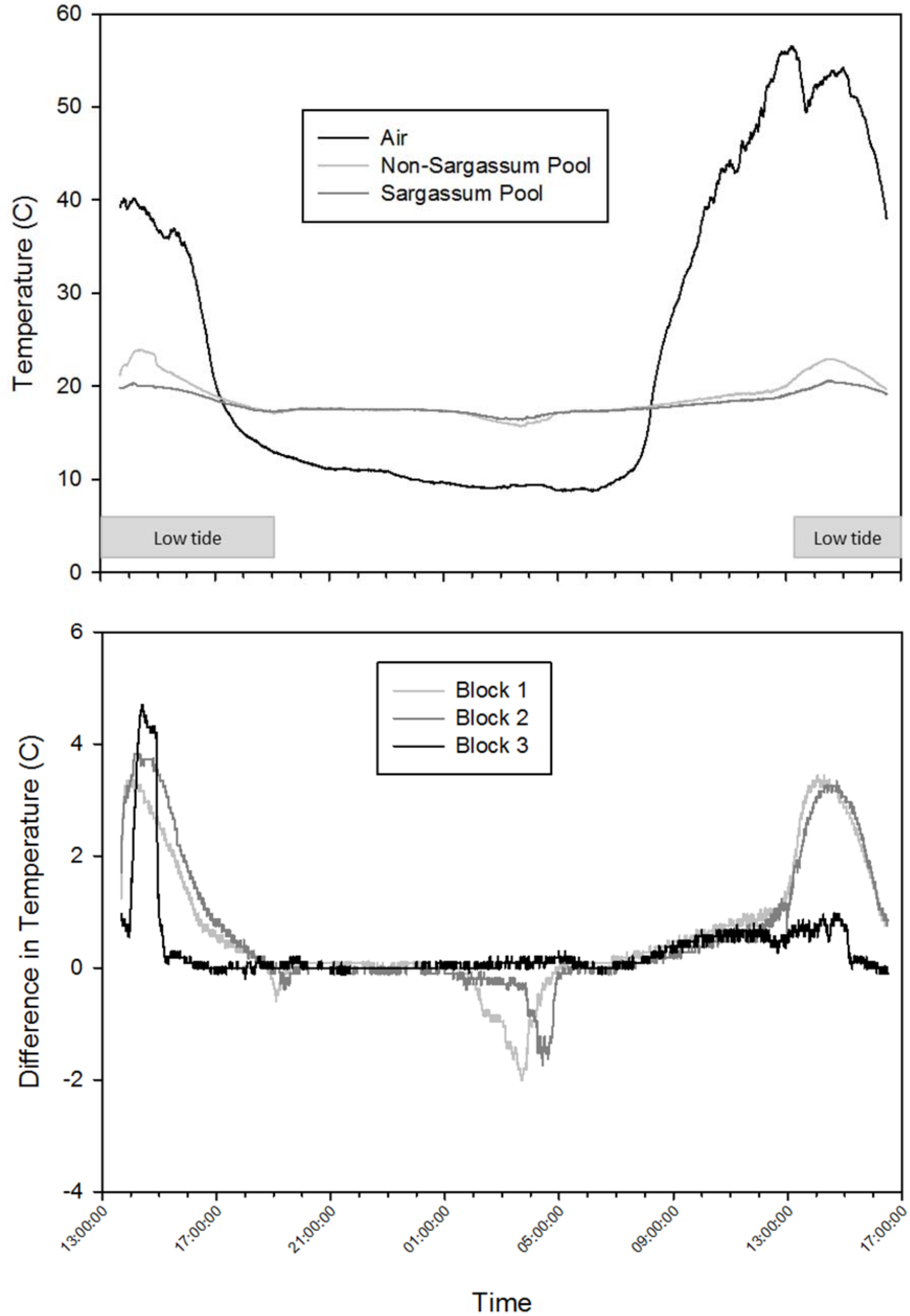

Figure 13. Mean temperature (°C) in air, in pools without *Sargassum*, and in pools with *Sargassum* in November 2013 is located in the upper figure. Indicated is the relative period of low tide when pools were no longer submerged. The difference in temperature (Non-*Sargassum* pools minus *Sargassum* pools) for paired blocks over time are located in the lower graph.

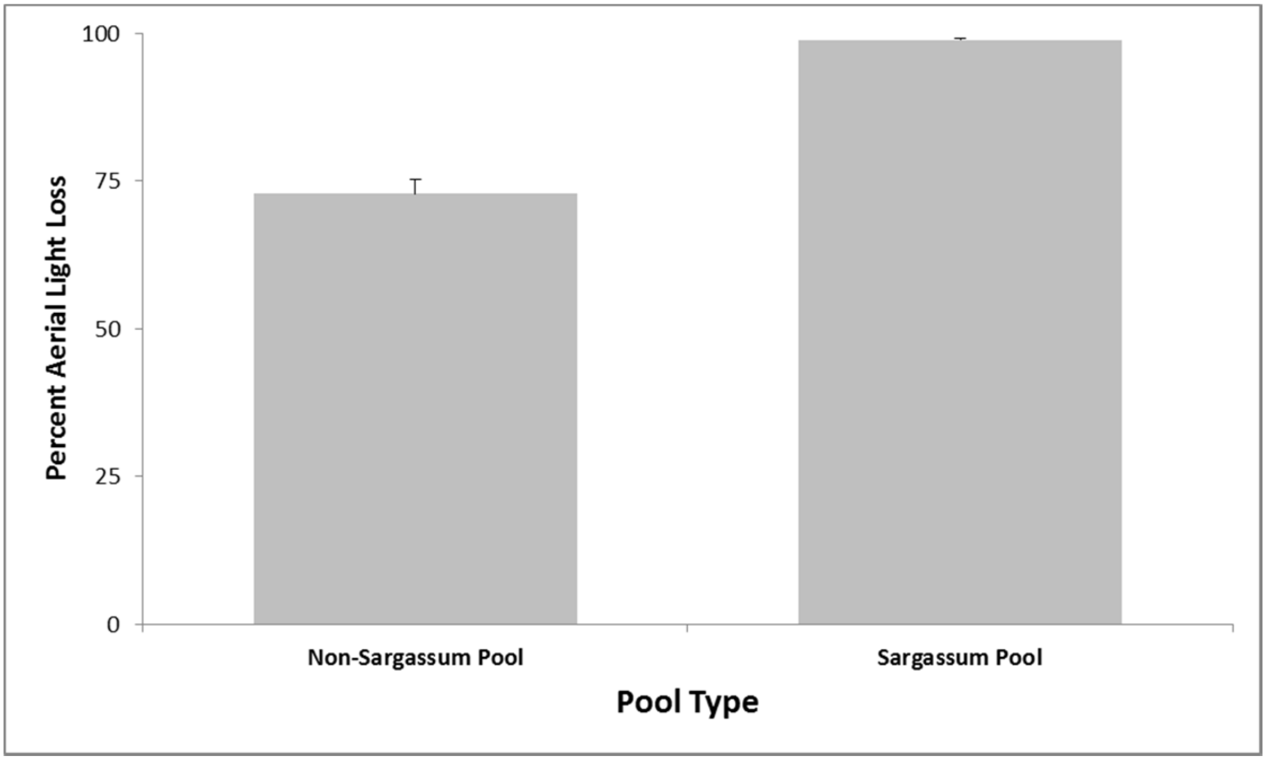

Figure 14. Mean percent aerial light loss (+/- SE) for tidepools with and without *Sargassum* present recorded during several intervals in February 2012 (t-test $p<0.001$).

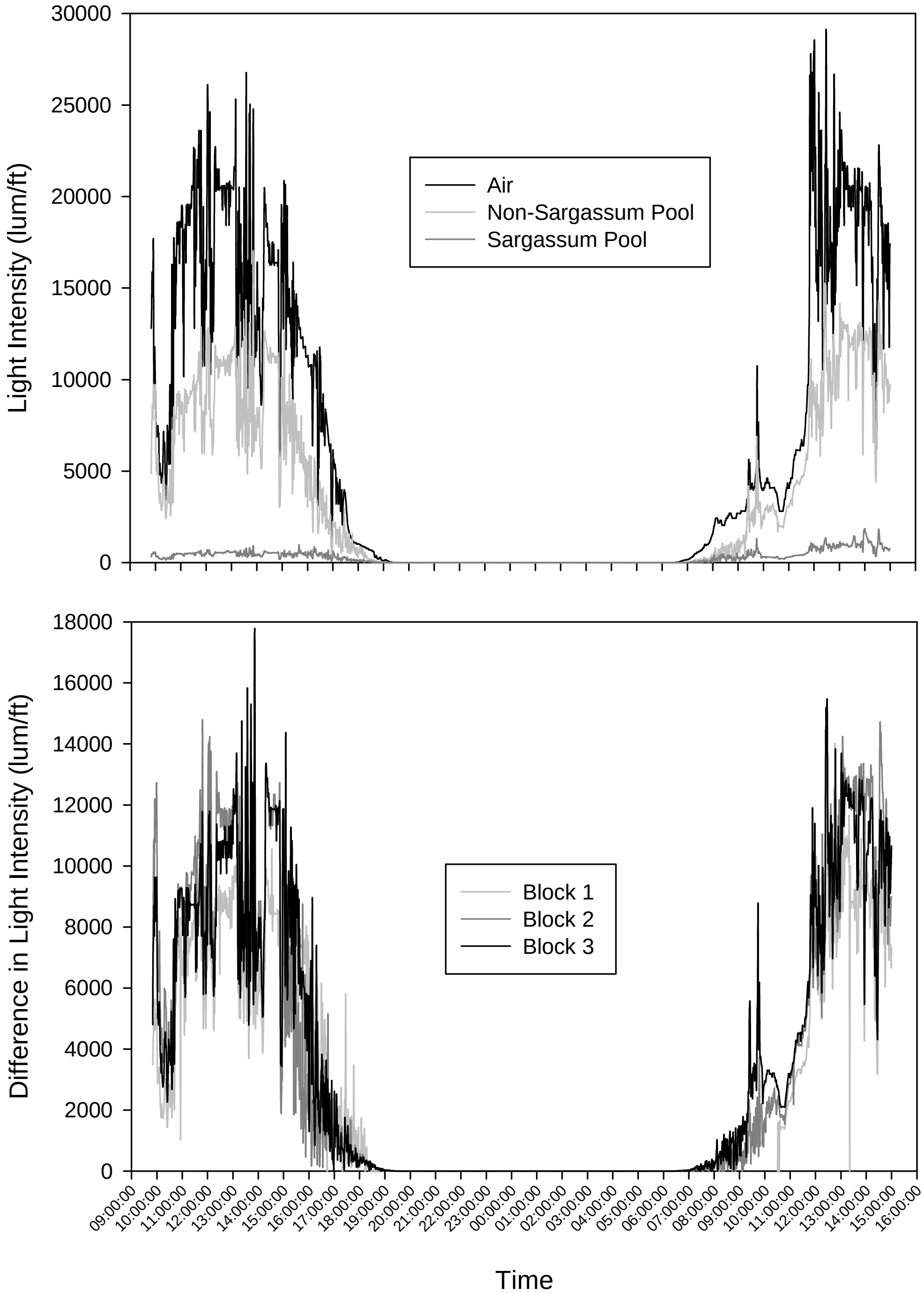

Figure 15. Mean light intensity (lum/ft) in air, in pools without *Sargassum* and in pools with *Sargassum* in April 2013 is located in the upper figure. The difference in light intensity (Non-*Sargassum* pools minus *Sargassum* pools) for paired blocks over time are located in the lower graph.

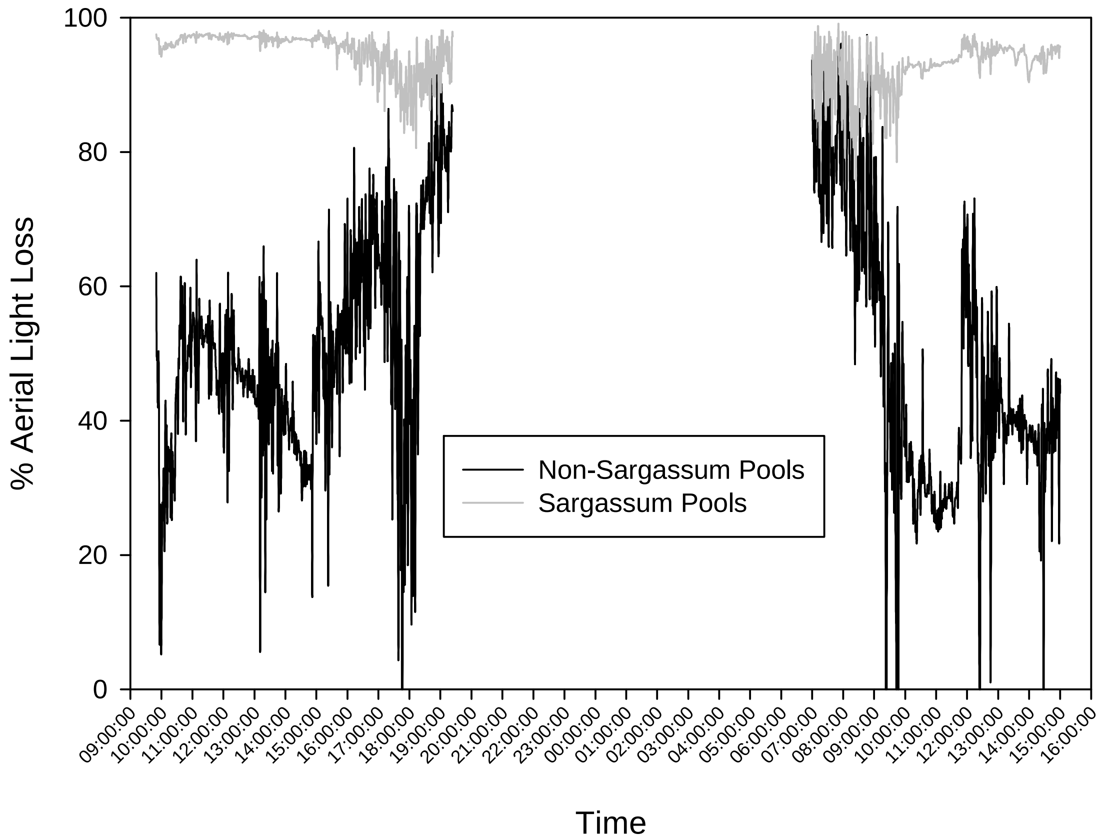

Figure 16. Mean % of aerial light lost in pools without *Sargassum* and with *Sargassum* in April 2013. Data during dark hours are not included.

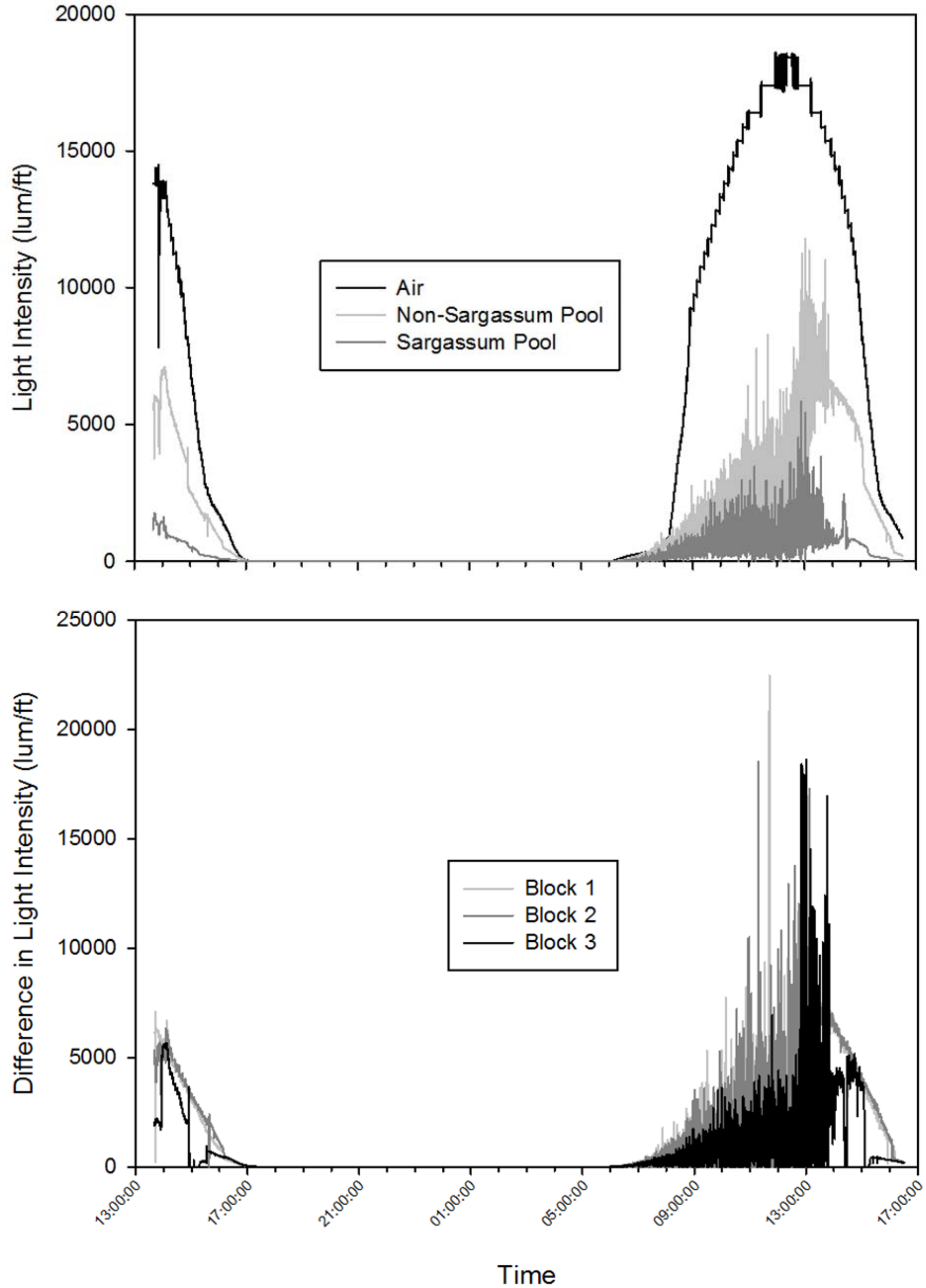

Figure 17. Mean light intensity (lum/ft) in air, in pools without *Sargassum* and in pools with *Sargassum* in November 2013 is located in the upper figure. The difference in light intensity (Non-*Sargassum* pools minus *Sargassum* pools) for paired blocks over time are located in the lower graph.

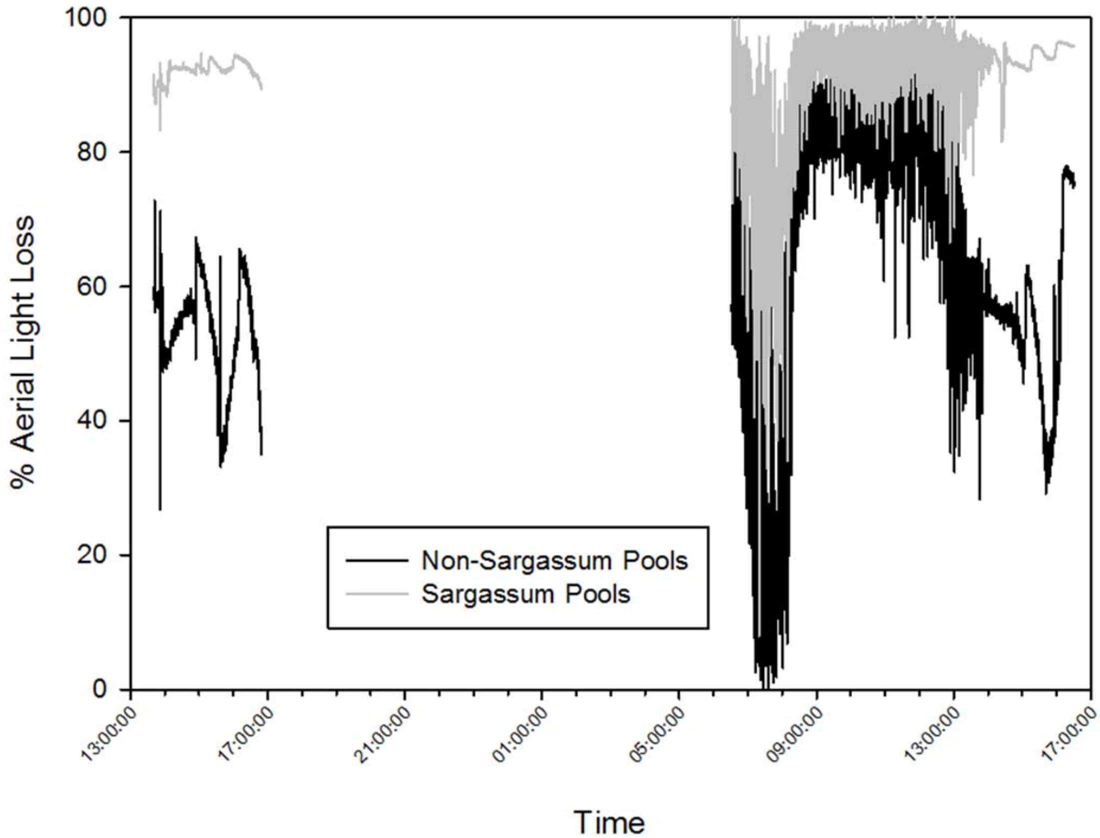

Figure 18. Mean % of aerial light lost in pools without *Sargassum* and with *Sargassum* in November 2013. Data during dark hours are not included.

3.13. Removal effort and success.

A total of 16.4 kg *Sargassum* (mean=1.2 kg) was removed from 14 plots while an extra 37.5 kg (mean=2.7 kg) were removed from the rest of the treatment tidepools. Therefore, together, a total of 54.0 kg (mean= 3.9 kg) was harvested in these 14 pools. For plots 0.35 m^2 in size, an average of 18.6 minutes were spent clearing plots with an average of ~50 holdfasts removed per plot (~30 second per holdfast). An average of 84.5 minutes was spent to clear the rest of the pools for a total of ~103 minutes spent clearing each pool. The size of the pools varied from 0.7 to 3.1 m^2 but the effort spent was more related to the number of holdfasts than the size of the pool. In total, a ~21 m^2 area was cleared for all 14 plots which required ~24 hours of effort (~1.15 hour per m^2).

The trajectory of *Sargassum* percent cover within plots from February 2012 to February 2013 (Figure 19) was significantly different among treatments:

Factor	df	F	p value
Treatment	3	181.1	<0.001
Plot (Treatment)	24	16.0	<0.001
Time	7	28.7	<0.001
Treatment * Time	21	7.7	<0.001

The control plots with no *Sargassum* did not vary much over time, reaching an average of 3% by the end of the experiment. *Sargassum* control plots exhibited a decline in cover naturally over the summer period and then recovered to reach similar cover to initial values in later winter. The two removal treatments exhibited a general steady increase in cover over time, following application of removal treatments in February 2012; the removal treatment with transplants had a slightly higher cover increase over time.

By the end of the experiment, the *Sargassum* plots (controls, removal, removal + transplant) contained similar cover of *Sargassum* but were significantly higher than the control plots (Figure 20; ANOVA, Treatment df=3, F=13.22, p<0.001; Block df=6, F=0.73, p=0.631; Tukey's multiple comparisons test). The *Sargassum* plots (ignoring non-*Sargassum* controls) were significantly similar by November (ANOVA *Sargassum* plots only, df=2, F=2.23, p=0.151; block df=6, F=2.1, p=0.130), just 9 months following application of removal treatments, suggesting that removal treatments had no long-term impact. Although final *Sargassum* cover was slightly lower than pretreatment (Figure 20), by the end of the experiment, cover change (pretreatment cover minus final cover) was similar in *Sargassum* plots for all three treatments (negative); however, non-*Sargassum* controls exhibited a slight increase in cover and were different that the *Sargassum* plots (ANOVA; Treatment df=3, F=3.07, p=0.05; block df=6, F=0.24, p=0.956; Tukey's multiple comparisons test). An example time series is visually shown for one plot showing pre-treatment cover, post removal cover, and cover 1 year following removal (Figure 21)

The transplanting of surfgrass, *Phyllospadix torreyi*, had no impact as removal+transplant treatments were the same as *Sargassum* control and removal treatments. In general, the surfgrass did not survive several early attempts at transplanting during the first month of the experiment. Although difficult to determine whether the surfgrass had an impact on recovery of *Sargassum* following removal and transplant, visual analyses of patterns of recovery and *Phyllospadix* cover over time in individual plots provides weak evidence that further experimentation could be needed (Figure 22). In the plots where *Phyllospadix* did survive at moderate levels, *Sargassum* cover remained relatively low over time. As *Phyllospadix* died off over time, *Sargassum* recovery appeared to reflect some delayed recovery. In plots where surfgrass died quickly, *Sargassum* recovery was relatively quick.

As discussed previously, there were few univariate or multivariate differences among *Sargassum* and non-*Sargassum* plots for both understory cover and macroinvertebrate counts (Section 3.11). Using the same data set for community assemblages, similar multivariate tests were conducted with treatments (non-*Sargassum* control, *Sargassum* control, removal, removal + transplant) as a factor in place of pool type (*Sargassum* vs. non-*Sargassum*); blocks were nested within Treatments but no block p value could be calculated. There were no differences in initial understory cover (Global R=-0.028, p=0.625) or macroinvertebrate counts (Global R=0.03, p=0.285) among treatments. The patterns observed in diversity were also similar whether *Sargassum* presence (Figure 9 above) or Treatment (Figure 23) was used as a fixed factor:

		Richness			Pielou's Evenness		
		df	F	p value	df	F	p value
Cover Data	*Sargassum* presence	1	0.41	0.528	1	0.94	0.345
	Block	6	0.93	0.496	6	4.17	**0.008**
	Treatment	3	0.86	0.481	3	0.87	0.479
	Block	6	1.08	0.415	6	4.10	**0.011**
Macroinvertebrate Counts	*Sargassum* presence	1	0.87	3.63	1	1.43	0.363
	Block	6	1.82	0.152	6	1.43	0.257
	Treatment	3	1.14	0.362	3	0.88	0.471
	Block	6	1.96	0.131	6	1.19	0.359

At the end of the year-long study, there were few patterns to be observed in the univariate data. For cover, there were no differences in taxa or functional groups/feeding guilds among treatments (Table 3) although the block effect was found to be significant on occasion. When combining *Sargassum* plots and comparing to non-*Sargassum* plots, few differences were observed, with the exception of higher cover in native plots of the red alga *Gelidium coulteri*, the limpets *Lottia scabra/conus* and *L. strigitella*, the chitons *Cyanoplex hartwegii* and *Nuttalina* spp., herbivores, and scavengers (Table 3). For macroinvertebrate counts, there were significantly more *L. scabra/conus* in the control plots while all other species were similar among treatments (Table 4). When comparing *Sargassum* and non-*Sargassum* plots, *L. scabra/conus*, *L. strigitella*, and *Nuttalina* spp. were significantly higher in non-*Sargassum* plots while the sea hare *Aplysia californica* was higher in *Sargassum* plots (Table 4).

Diversity at the end of the year-long study was similar among treatments for cover and macroinvertebrate densities (Figure 24). Whether analyzing diversity data by the Treatment factor or the Pool Type factor (Figure 25), diversity values were similar for all data sets; blocks showed varied significance depending on the analyses:

		Richness			Pielou's Evenness		
		df	F	p value	df	F	p value
Cover Data	*Sargassum* presence	1	2.49	0.133	1	0.00	0.994
	Block	6	1.07	0.417	6	2.07	0.111
	Treatment	3	2.42	0.107	3	0.84	0.492
	Block	6	1.20	0.360	6	2.34	0.085
Macroinvertebrate Counts	*Sargassum* presence	1	2.82	0.112	1	2.77	0.114
	Block	6	3.07	**0.032**	6	3.94	**0.012**
	Treatment	3	0.99	0.425	3	1.37	0.290
	Block	6	2.77	**0.051**	6	3.49	**0.023**

For community assemblages, there were no differences among treatments for cover data (Figure 26, ANOSIM Global R=-0.018, p=0.562); no block effect could be analyzed. When combining *Sargassum* plots and comparing to non-*Sargassum* pools, community structure was again similar (ANOSIM Global R=0.016; p=0.340); however, a significant block effect was observed (ANOSIM Global R=0.434; p=0.003). Similar patterns were observed in the macroinvertebrate count community assemblage analyses (Figure 27) where community structure was similar among treatments (ANOSIM Global R=-0.002, p=0.483); no block effect could be analyzed. Equally, no difference was observed in pool type (ANOSIM Global R=0.021; p=0.350), though a significant block effect was observed (ANOSIM Global R=0.368; p=0.003).

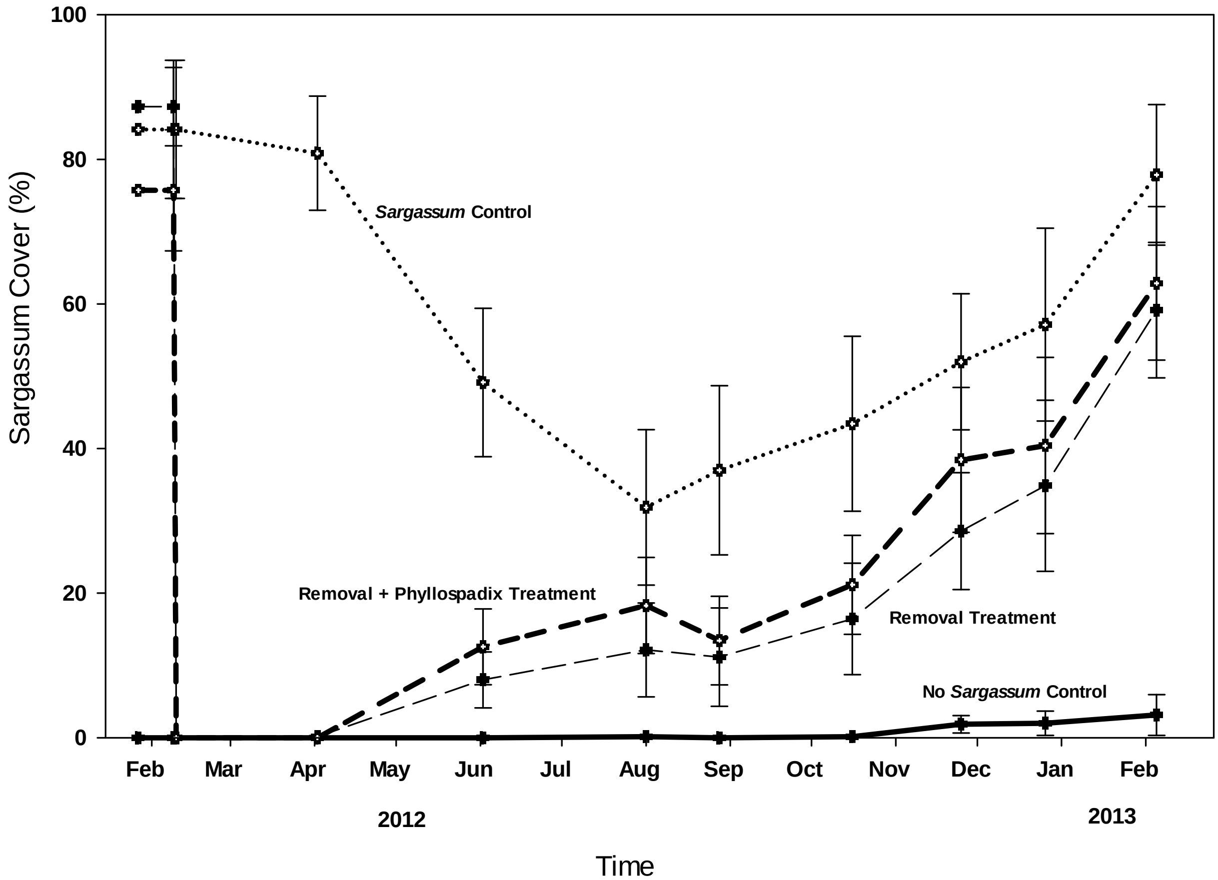

Figure 19. Mean *Sargassum* cover (+/- SE) for the four treatments prior to application of removal treatments and for one year following. The trajectories of cover over time were significantly different (Repeated Measures ANOVA).

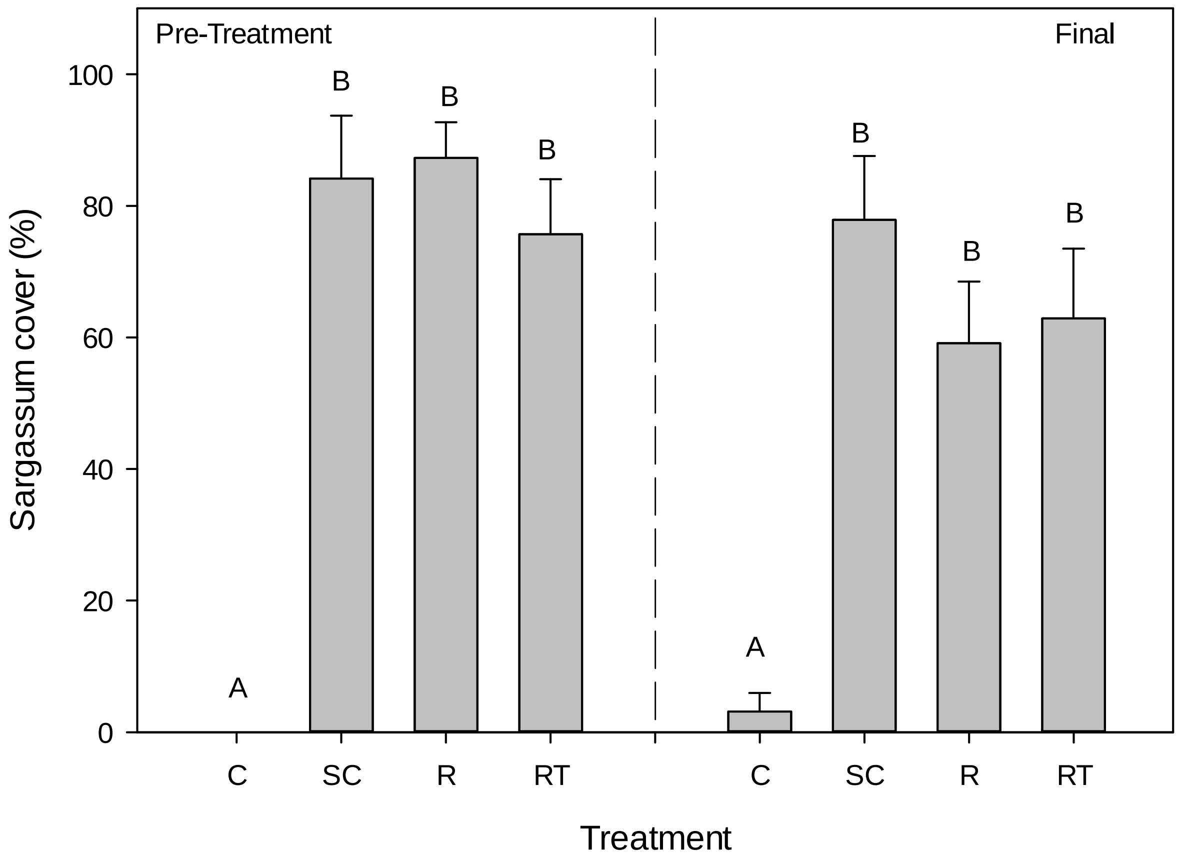

Figure 20. Mean *Sargassum* cover (+/- SE) for the four treatments prior to application of treatments (Pre-Treatment) and at the end of the experiment 1 year later (Final). Treatments were significantly different from each other for separate ANOVA analyses for the two time periods. Letters above bars represent Tukey's multiple comparisons results whereby letters signifying significantly different groups for both analyses. *Sargassum* plots were similar during the period before application of treatments and at the end of the experiment.

February 2012 Pre-Removal

February 2012 Post-Removal

February 2013 - 1 year later

Figure 21. Example of *Sargassum* cover in one plot prior to removal, immediately after removal, and 1 year later.

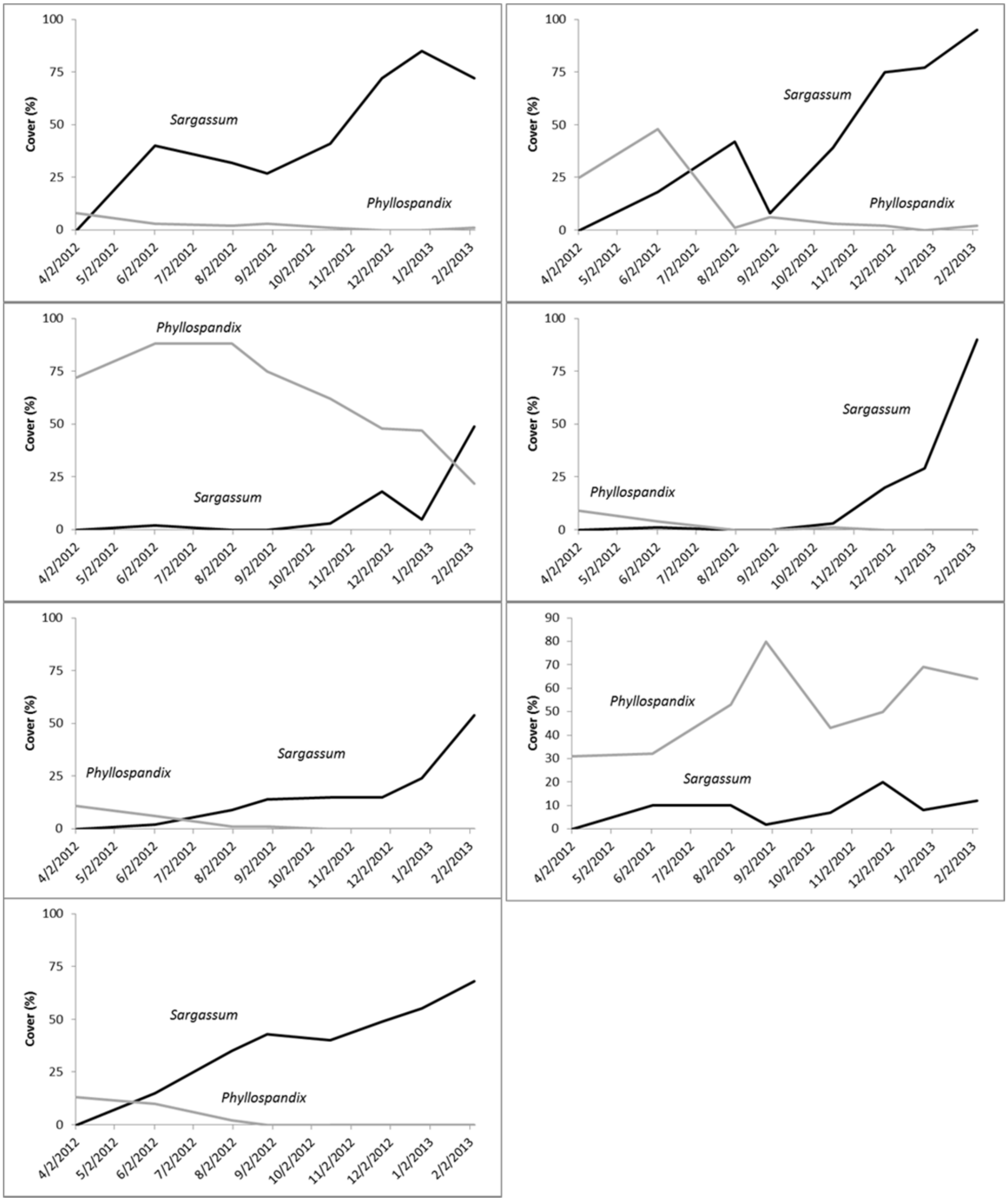

Figure 22. Cover of *Sargassum* and the surfgrass *Phyllospadix* over time in individual plots following *Sargassum* removal and transplanting of *Phyllospadix*.

Table 3. Mean (+/- SE) percent cover of abiotic, seaweed, macroinvertebrate, and functional group/feeding guild for the four treatments (SC=*Sargassum* control, R=Removal Treatment, RT=Removal Treatment + Surfgrass Transplant, C=Non-*Sargassum* Control) and for Native Pools (Non-*Sargassum* control) and all *Sargassum* treatments (pools) combined. Reported are the p values for two sets of ANOVAs (Treatment or *Sargassum* presence (fixed factor) and block (random factor)).

									ANOVA pvalues						ANOVA pvalues	
	SC Mean	SC SE	R Mean	R SE	RT Mean	RT SE	C Mean	C SE	Treatment (Fixed Factor)	Block (Random Factor)	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	Sargassum/No Sargassum (Fixed Factor)	Block (Random Factor)
Abiotic																
Rock	10.6	6.5	14.7	4.3	29.0	9.8	16.4	4.4	0.166	0.800	16.4	4.4	18.1	4.3	0.812	0.123
Sand	11.2	7.1	4.0	2.0	4.9	3.1	2.9	1.9	0.518	0.592	2.9	1.9	6.7	2.6	0.439	0.584
Seaweed:																
Acrosorium ciliolatum	0.7	0.3	0.9	0.9	0.9	0.3	0.0	0.0	0.472	0.146	0.0	0.0	0.8	0.3	0.108	0.106
Centrocera clavulatum	0.1	0.1	0.0	0.0	0.0	0.0	2.0	1.8	0.343	0.343	2.0	1.8	0.0	0.0	0.061	0.282
Ceramium spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.415	0.455	0.1	0.1	0.0	0.0	0.083	0.391
Chondracanthus canaliculatus	1.0	0.8	0.0	0.0	0.1	0.1	0.0	0.0	0.327	0.506	0.0	0.0	0.4	0.3	0.467	0.536
Corallina pinnatifolia/vancouveriensis	45.7	10.1	50.7	7.8	36.5	8.3	46.4	10.3	0.707	0.264	46.4	10.3	44.3	5.0	0.835	0.243
Crustose Coralline	8.5	3.5	5.9	3.2	8.7	4.1	11.2	5.3	0.538	**0.000**	11.2	5.3	7.7	2.0	0.229	**0.000**
Cryptopleura crispa	0.1	0.1	0.7	0.7	0.1	0.1	0.7	0.7	0.725	0.313	0.7	0.7	0.3	0.2	0.485	0.277
Dictypoteris undulata	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1	0.604	0.590	0.1	0.1	0.0	0.0	0.428	0.568
Dictyota coriaceum	4.3	3.4	2.4	1.2	2.9	1.1	4.1	1.7	0.873	0.169	4.1	1.7	3.2	1.2	0.683	0.134
Dictyota flabellata	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472
Gelidium coulteri	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.7	0.108	0.455	1.0	0.7	0.0	0.0	**0.011**	0.391
Gelidium pusillum	0.1	0.1	0.3	0.3	0.5	0.5	0.1	0.1	0.814	0.235	0.1	0.1	0.3	0.2	0.626	0.199
Laurencia pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.415	0.455	0.1	0.1	0.0	0.0	0.083	0.391
Lithothrix aspergillum	8.9	4.5	10.1	8.7	9.0	6.4	9.7	7.3	0.997	**0.003**	9.7	7.3	9.3	3.7	0.943	**0.001**
Osmundea sinicola	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.415	0.455	0.1	0.1	0.0	0.0	0.083	0.391
Phyllospadix shoots and roots	0.0	0.0	0.0	0.0	1.4	1.4	0.0	0.0	0.415	0.455	0.0	0.0	0.5	0.5	0.576	0.472
Psuedolithoderma/Ralfsia	9.8	2.4	8.9	6.2	2.3	1.2	11.3	4.0	0.209	**0.018**	11.3	4.0	7.0	2.3	0.251	**0.021**
Pterocladiella capillacea	3.6	1.7	5.4	2.1	3.1	1.5	1.7	0.9	0.450	0.381	1.7	0.9	4.0	1.0	0.212	0.353
Sargassum muticum holdfast	4.2	2.7	1.3	0.7	0.9	0.8	0.0	0.0	0.222	0.392	0.0	0.0	2.1	1.0	0.222	0.421
Ulva californica	0.7	0.5	0.9	0.5	0.3	0.2	0.7	0.6	0.840	0.736	0.7	0.6	0.6	0.2	0.858	0.708
Jania crassa	0.0	0.0	0.4	0.4	0.7	0.7	0.0	0.0	0.580	0.574	0.0	0.0	0.4	0.3	0.442	0.556
Hypnea valentiae	0.1	0.1	0.0	0.0	0.0	0.0	0.7	0.7	0.483	0.506	0.7	0.7	0.0	0.0	0.115	0.445
Colpomenia sinuosa	0.6	0.6	0.9	0.3	0.9	0.5	0.7	0.5	0.964	0.317	0.7	0.5	0.8	0.3	0.925	0.264
Lomentaria hakodotensis	0.0	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.102	0.455	0.0	0.0	0.1	0.1	0.428	0.568
Chaetomorpha linum	0.1	0.1	0.0	0.0	0.0	0.0	0.3	0.3	0.563	0.562	0.3	0.3	0.0	0.0	0.204	0.516
Caulacanthus ustulatus	0.0	0.0	0.0	0.0	0.3	0.3	0.4	0.4	0.588	0.579	0.4	0.4	0.1	0.1	0.273	0.542
Cladophora spp	0.0	0.0	0.0	0.0	0.1	0.1	0.3	0.3	0.415	0.065	0.3	0.3	0.0	0.0	0.135	**0.049**
Silvetia compressa	0.0	0.0	1.9	1.7	0.0	0.0	0.0	0.0	0.339	0.455	0.0	0.0	0.6	0.6	0.546	0.487
Ectocarpus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.415	0.455	0.7	0.7	0.0	0.0	0.083	0.391
Egregia menziesii	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.415	0.455	0.0	0.0	0.1	0.1	0.576	0.472
Amphiroa ciolatum	0.1	0.1	0.4	0.4	0.3	0.2	0.0	0.0	0.463	**0.024**	0.0	0.0	0.3	0.2	0.208	**0.017**
Scytosiphon dotyi	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.1	0.1	0.576	0.472

Table 3 continued.

	SC Mean	SC SE	R Mean	R SE	RT Mean	RT SE	C Mean	C SE	ANOVA pvalues Treatment (Fixed Factor)	ANOVA pvalues Block (Random Factor)	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	ANOVA pvalues Sargassum/No Sargassum (Fixed Factor)	ANOVA pvalues Block (Random Factor)
Invertebrates:																
Agathostoma eiseni	0.4	0.1	0.2	0.1	0.1	0.1	0.3	0.1	0.298	0.532	0.3	0.1	0.2	0.1	0.619	0.576
Anthopleura sola/elegantissima	0.6	0.6	0.6	0.3	1.7	0.8	2.7	1.4	0.201	0.103	2.7	1.4	1.0	0.4	0.063	0.089
Chlorostoma aureotincta	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472
Chlorostoma funebralis	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.3	0.319	**0.001**	0.4	0.3	0.1	0.1	0.066	**0.000**
Cyanoplax hartwegii	0.0	0.0	0.1	0.1	0.1	0.1	0.2	0.1	0.157	0.125	0.2	0.1	0.0	0.0	**0.032**	0.101
Littorina spp.	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472
Lottia limatula	0.2	0.2	0.4	0.1	0.7	0.4	0.4	0.1	0.611	0.352	0.4	0.1	0.4	0.1	0.990	0.344
Lottia scabra/conus	0.2	0.1	0.2	0.1	0.2	0.1	0.4	0.1	0.135	0.076	0.4	0.1	0.2	0.1	**0.020**	0.054
Mytilus californianus	0.0	0.0	1.9	1.9	0.0	0.0	0.3	0.3	0.415	0.252	0.3	0.3	0.6	0.6	0.755	0.269
Nuttalina spp.	0.1	0.1	0.2	0.1	0.2	0.1	0.4	0.1	0.114	**0.007**	0.4	0.1	0.1	0.1	**0.030**	**0.005**
Pachygrapsus crassipes	0.0	0.0	0.1	0.1	0.3	0.2	0.2	0.1	0.271	0.613	0.2	0.1	0.1	0.1	0.596	0.661
Pagurus spp.	0.4	0.2	0.2	0.1	1.3	1.1	0.7	0.4	0.610	0.342	0.7	0.4	0.6	0.4	0.920	0.333
Sculpin	0.2	0.1	0.1	0.1	0.4	0.1	0.1	0.1	0.118	**0.019**	0.1	0.1	0.2	0.1	0.636	0.038
Strongylocentrotus purpuratus	0.3	0.2	0.4	0.3	0.8	0.5	2.9	2.7	0.517	0.329	2.9	2.7	0.5	0.2	0.128	0.270
Lottia strigitella	0.2	0.1	0.4	0.1	0.2	0.1	0.5	0.1	0.057	0.070	0.5	0.1	0.2	0.1	**0.022**	0.073
Unidentified shrimp	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.752	0.537	0.1	0.1	0.1	0.1	0.983	0.512
Lepidizona spp.	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.732	0.379	0.1	0.1	0.2	0.1	0.968	0.355
Aplysia californica	0.3	0.2	0.9	0.7	0.4	0.3	0.0	0.0	0.281	0.060	0.0	0.0	0.5	0.3	0.168	0.056
Fissurella volcano	0.1	0.1	0.0	0.0	0.1	0.1	0.1	0.1	0.598	0.818	0.1	0.1	0.0	0.0	0.251	0.794
Phragmatopoma californica	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.415	**0.033**	0.1	0.1	0.0	0.0	0.329	**0.029**
Mopalia muscosa	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472
Ceratostoma spp.	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472
Epitonium tinctum	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.415	0.455	0.1	0.1	0.0	0.0	0.083	0.391

Table 3 continued.

	SC Mean	SC SE	R Mean	R SE	RT Mean	RT SE	C Mean	C SE	ANOVA pvalues: Treatment (Fixed Factor)	ANOVA pvalues: Block (Random Factor)	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	ANOVA pvalues: Sargassum/No Sargassum (Fixed Factor)	ANOVA pvalues: Block (Random Factor)
Functional Groups:																
Abiotic	21.8	8.3	18.7	5.5	33.8	8.9	19.2	4.9	0.330	**0.041**	19.2	4.9	24.8	4.5	0.554	**0.046**
Sheet Algae	1.6	0.8	2.4	1.2	1.3	0.5	1.5	0.8	0.299	0.324	1.5	0.8	1.8	0.5	0.081	0.286
Articulate Corallines	54.7	12.9	61.7	12.2	46.5	13.0	56.1	16.4	0.410	0.568	56.1	16.4	54.3	7.1	0.746	0.592
Filamentous-like Algae	0.3	0.2	0.0	0.0	0.1	0.1	3.4	2.8	0.415	0.283	3.4	2.8	0.1	0.1	0.751	0.302
Encrusting Algae	18.3	4.0	14.7	6.9	11.0	4.7	22.5	6.4	0.376	0.555	22.5	6.4	14.7	3.0	0.574	0.474
Fleshy Algae	9.9	5.7	9.4	2.5	7.9	1.5	9.2	3.0	0.439	0.370	9.2	3.0	9.1	2.0	0.335	0.362
Seagrass	0.0	0.0	0.0	0.0	1.4	1.4	0.0	0.0	0.415	0.455	0.0	0.0	0.5	0.5	0.576	0.482
Tough and Leathery Algae	4.2	2.7	3.1	1.7	1.2	0.8	0.0	0.0	0.220	0.325	0.0	0.0	2.9	1.1	0.134	0.330
Herbivores	2.4	0.8	3.1	0.9	3.2	0.8	5.9	2.8	0.256	0.611	5.9	2.8	2.9	0.5	**0.041**	0.555
Scavengers	1.1	0.7	0.9	0.4	3.3	1.3	3.6	1.8	0.085	0.323	3.6	1.8	1.8	0.5	**0.015**	0.290
Filter Feeders	0.0	0.0	1.9	1.9	0.1	0.1	0.4	0.3	0.333	0.504	0.4	0.3	0.7	0.6	0.583	0.539
Predators	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1	0.604	0.590	0.1	0.1	0.0	0.0	0.428	0.568
Fish	0.2	0.1	0.1	0.1	0.4	0.1	0.1	0.1	0.928	0.507	0.1	0.1	0.2	0.1	0.725	0.454

Table 4. Mean (+/- SE) counts of macroinvertebrates for the four treatments (SC=*Sargassum* control, R=Removal Treatment, RT=Removal Treatment + Surfgrass Transplant, C=Non-*Sargassum* Control) and for Native Pools (Non-*Sargassum* control) and all *Sargassum* treatments (pools) combined. Reported are the p values for two sets of ANOVAs (Treatment or *Sargassum* presence (fixed factor) and block (random factor)).

									ANOVA pvalues						ANOVA pvalues	
	SC Mean	SC SE	R Mean	R SE	RT Mean	RT SE	C Mean	C SE	Treatment (Fixed Factor)	Block (Random Factor)	Native Pool Mean	Native Pool SE	*Sargassum* Pool Mean	*Sargassum* Pool SE	Sargassum/No Sargassum (Fixed Factor)	Block (Random Factor)
Agathostoma eiseni	3.4	2.4	0.6	0.3	0.7	0.7	2.6	1.6	0.511	0.685	2.6	1.6	1.6	0.9	0.589	0.687
Chlorostoma aureotincta	0.0	0.0	0.0	0.0	0.6	0.6	0.0	0.0	0.415	0.455	0.0	0.0	0.2	0.2	0.576	0.472
Chlorostoma funebralis	4.9	3.6	0.1	0.1	3.3	3.3	1.4	1.3	0.481	0.110	1.4	1.3	2.8	1.6	0.614	0.109
Cyanoplax hartwegii	0.0	0.0	0.1	0.1	0.3	0.3	1.1	0.8	0.215	0.133	1.1	0.8	0.1	0.1	**0.035**	0.099
Littorina spp.	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.1	0.1	0.576	0.472
Lottia limatula	1.0	0.7	3.1	2.2	3.9	1.9	2.4	0.8	0.603	0.512	2.4	0.8	2.7	1.0	0.894	0.507
Lottia scabra/conus	0.9	0.7	3.7	2.3	4.7	3.0	14.6	6.1	**0.045**	0.139	14.6	6.1	3.1	1.3	**0.005**	0.112
Nuttalina spp.	0.3	0.3	2.3	1.8	2.4	1.6	6.3	3.5	0.156	**0.045**	6.3	3.5	1.7	0.8	**0.032**	**0.033**
Pachygrapsus crassipes	0.0	0.0	0.3	0.2	0.7	0.4	0.6	0.3	0.212	0.375	0.6	0.3	0.3	0.1	0.437	0.433
Pagurus samuelis	4.4	2.6	2.1	1.2	11.3	10.3	3.3	0.9	0.608	0.323	3.3	0.9	6.0	3.5	0.659	0.309
Sculpin	0.3	0.2	0.1	0.1	0.6	0.2	0.3	0.2	0.297	0.080	0.3	0.2	0.3	0.1	0.803	0.099
Strongylocentrotus purpuratus	1.0	0.8	1.1	0.7	3.0	1.9	8.1	7.8	0.556	0.342	8.1	7.8	1.7	0.7	0.155	0.285
Lottia strigitella	1.4	0.9	3.7	1.2	9.0	5.0	20.1	11.5	0.195	0.463	20.1	11.5	4.7	1.8	**0.041**	0.423
Unidentified shrimp	0.1	0.1	1.6	1.4	1.9	1.2	1.1	1.0	0.664	0.385	1.1	1.0	1.2	0.6	0.968	0.370
Lepidizona spp.	0.4	0.4	0.3	0.3	0.4	0.4	0.6	0.4	0.969	0.550	0.6	0.4	0.4	0.2	0.673	0.490
Aplysia californica	0.3	0.2	0.7	0.4	0.4	0.3	0.0	0.0	0.102	**0.003**	0.0	0.0	0.5	0.2	**0.047**	**0.003**
Fissurella volcano	0.1	0.1	0.0	0.0	0.1	0.1	0.4	0.3	0.465	0.755	0.4	0.3	0.1	0.1	0.130	0.718
Unidentified snail Epitonium like	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.415	0.455	0.1	0.1	0.0	0.0	0.083	0.391
Ceratastoma	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.415	**0.033**	0.0	0.0	0.1	0.1	0.329	**0.029**
Mopalia muscosa	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.415	0.455	0.0	0.0	0.0	0.0	0.576	0.472

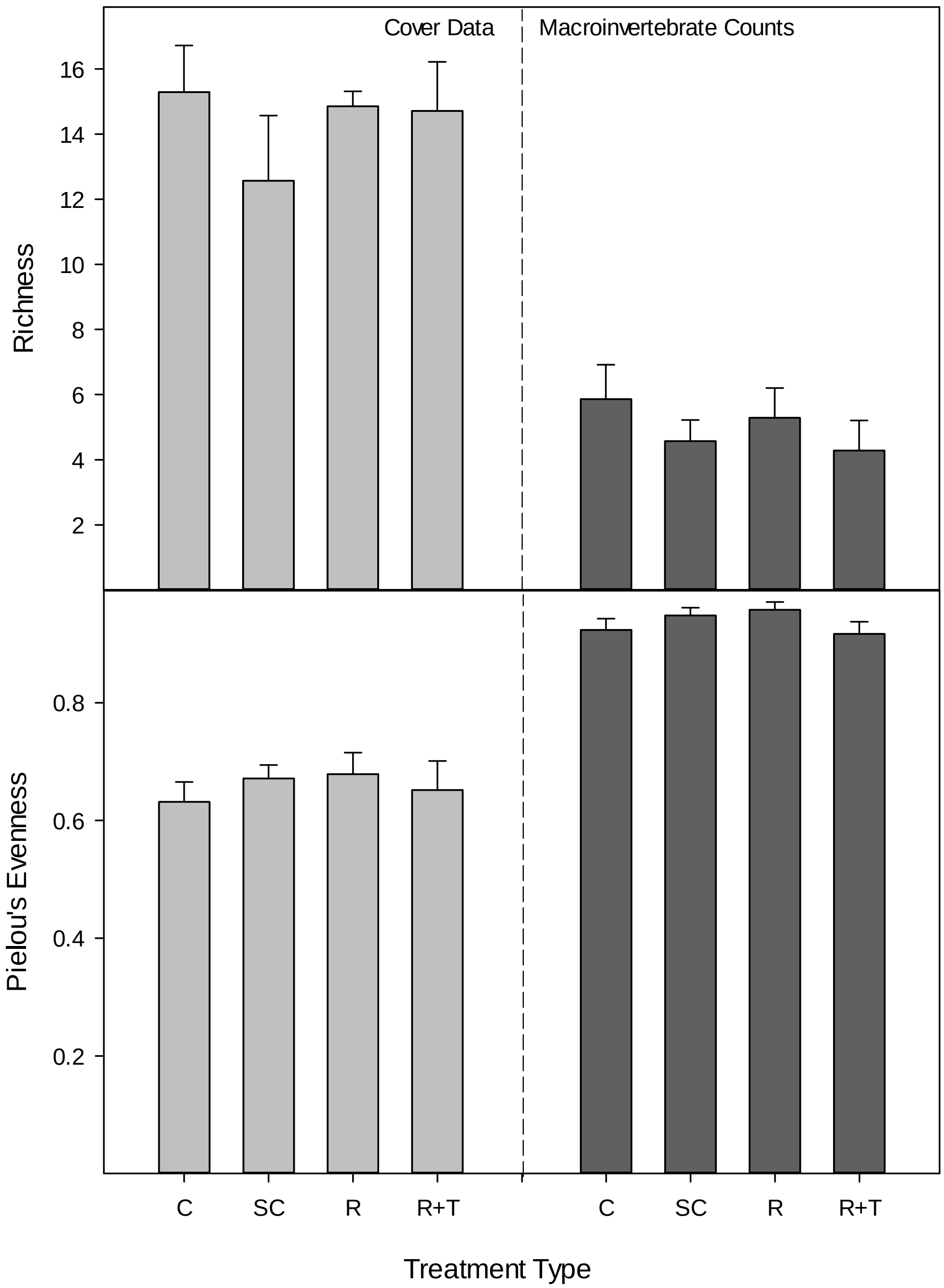

Figure 23. Mean species diversity (richness (upper figure) and Pielou's Evenness (lower figure)) (+/- SE) among treatments for cover data (left) and macroinvertebrate counts (right) at the beginning of the study before application of treatments. No significant difference was observed within any data set (ANOVA Treatment $p>0.05$; block $p>0.05$ except for Pielou's Evenness for cover data $p=0.011$).

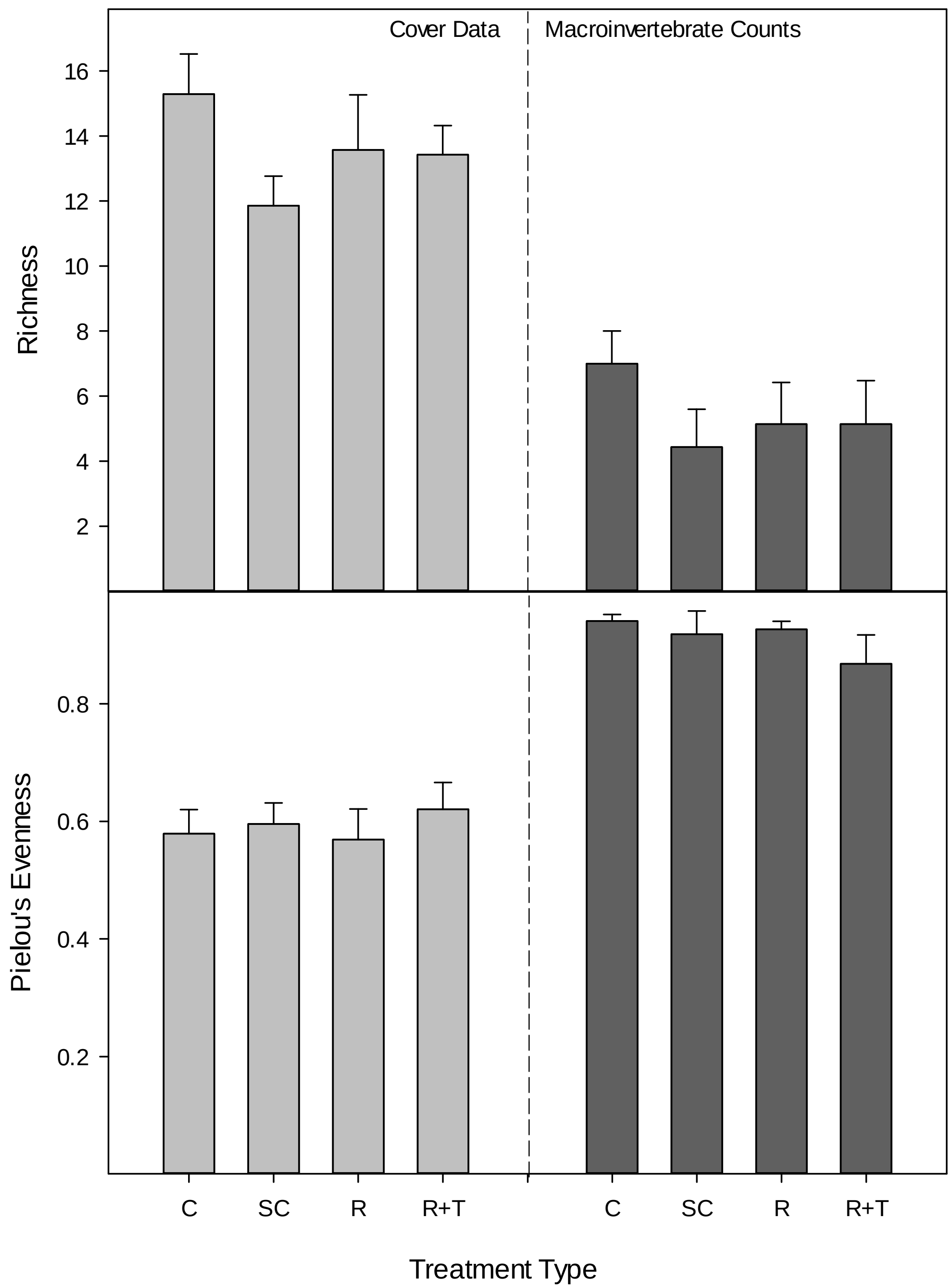

Figure 24. Mean species diversity (richness (upper figure) and Pielou's Evenness (lower figure)) (+/- SE) among treatments for cover data (left) and macroinvertebrate counts (right) at the end of the year-long study. No significant difference was observed within any data set (ANOVA Treatment $p>0.05$; block $p>0.05$ except for richness $p=0.051$and Pielou's Evenness for Macroinvertebrate counts $p=0.023$).

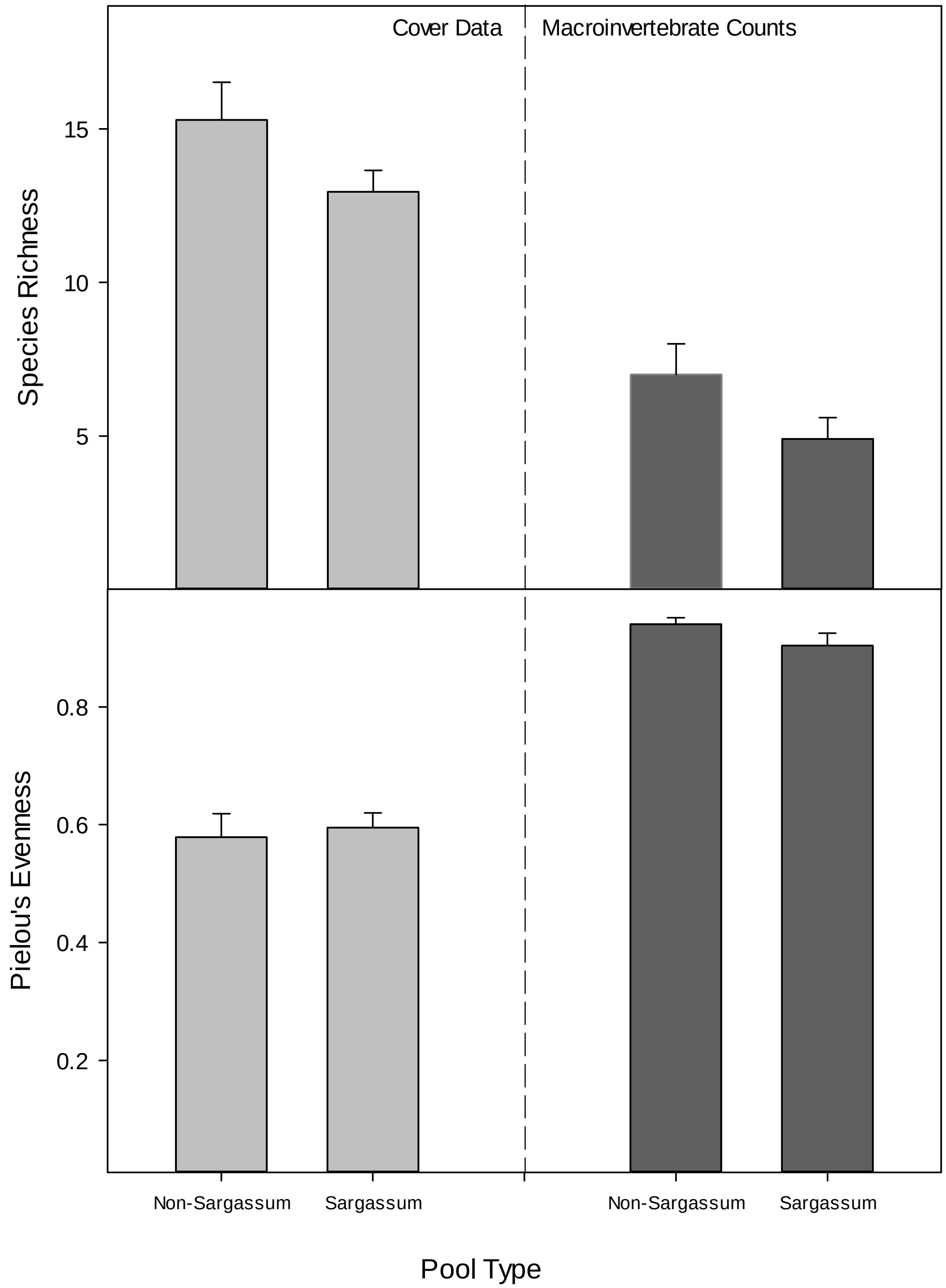

Figure 25. Mean species diversity (richness (upper figure) and Pielou's Evenness (lower figure)) (+/- SE) between pool types for cover data (left) and macroinvertebrate counts (right) at the end of the year-long study. No significant difference was observed within any data set (ANOVA Treatment $p>0.05$; block $p>0.05$ except for richness ($p=0.032$) and Pielou's Evenness for Macroinvertebrate counts ($p=0.012$)).

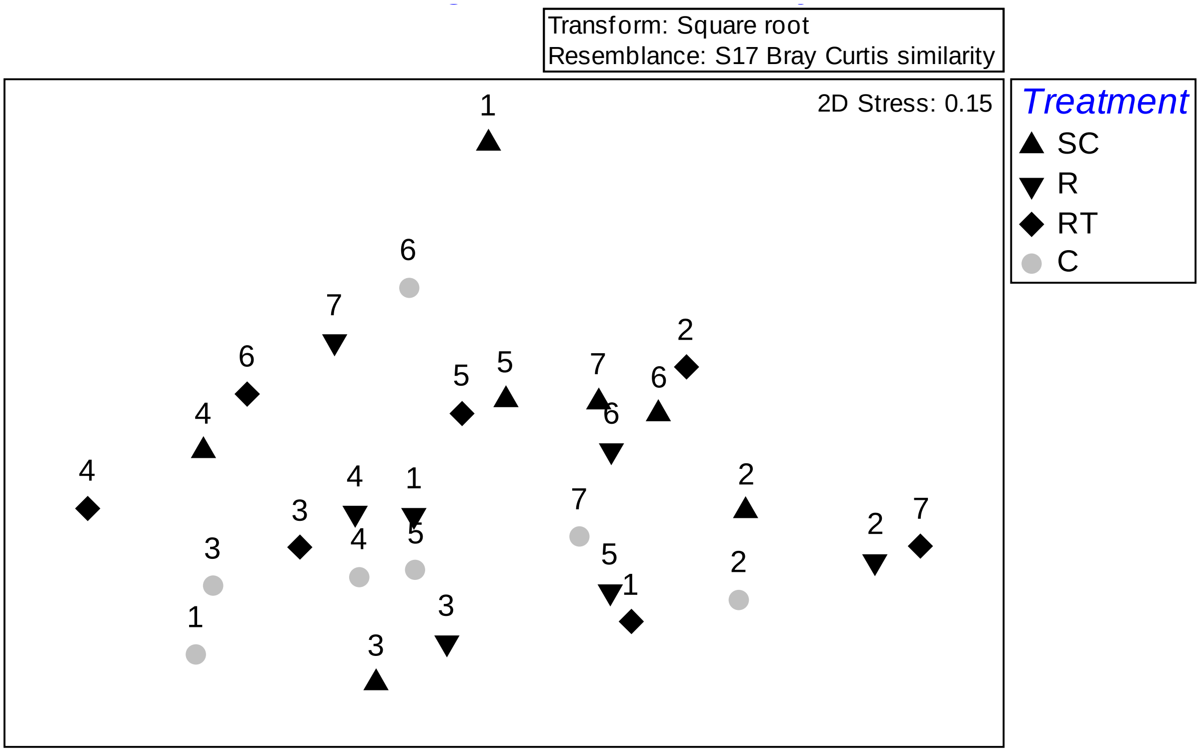

Figure 26. Multidimensional scaling plot of community structure using percent cover data in treatment plots (SC=*Sargassum* Control, R=*Sargassum* Removal, RT=*Sargassum* Removal + *Phyllospadix* Transplant, C=Non-*Sargassum* Control) at the end of the year-long study. Block numbers are labelled. Community structure was similar among treatments (ANOSIM Global R= -0.018, p=0.562); no block effect could be analyzed. When combining the *Sargassum* treatments (black symbols) as *Sargassum* pools and comparing to control plots without *Sargassum* (grey circles), no difference was observed in pool type (ANOSIM Global R=0.016; p=0.340); a significant block effect was observed (ANOSIM Global R=0.434; p=0.003).

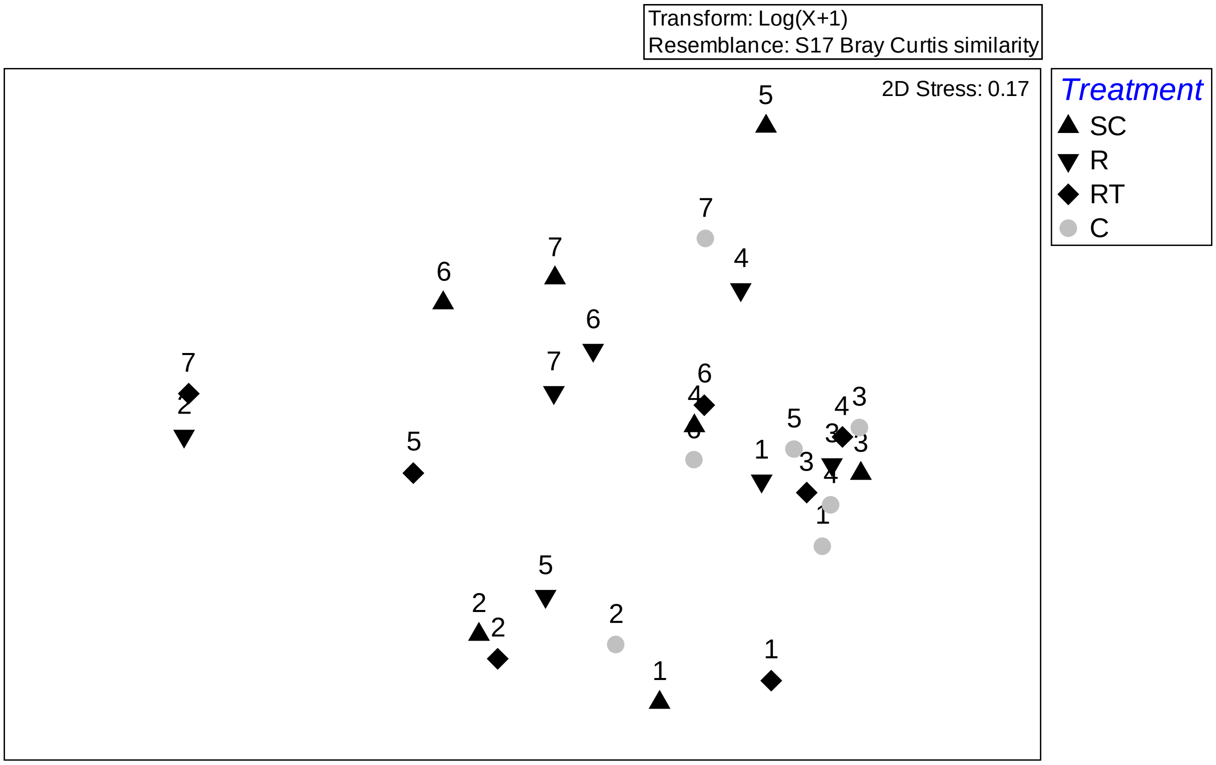

Figure 27. Multidimensional scaling plot of community structure using mobile invertebrate counts data in treatment plots (SC=*Sargassum* Control, R=*Sargassum* Removal, RT=*Sargassum* Removal + *Phyllospadix* Transplant, C=Non-*Sargassum* Control) at the end of the year-long study. Block numbers are labelled. Community structure was similar among treatments (ANOSIM Global R=-0.002, p=0.483); no block effect could be analyzed. When combining the *Sargassum* treatments (black symbols) as *Sargassum* pools and comparing to control plots without *Sargassum* (grey circles), no difference was observed in pool type (ANOSIM Global R=0.021; p=0.350); a significant block effect was observed (ANOSIM Global R=0.368; p=0.003).

3.14. Phlorotannin concentrations.

The phlorotannin concentrations of *S. muticum* individuals among tidal zones were similar to one another (ANOVA, df=2, F=0.22, p=0.802) with the mean concentration of approximately 5.85 phlorotannin %Dry Mass (Figure 28). Although the concentrations were similar to one another, individuals that were collected from the low intertidal zone ranked with the highest concentration of phlorotannins and individuals collected from the mid intertidal ranked with the lowest concentration. In each zone there was substantial variation in phlorotannin concentration among individuals collected from a single tidal height.

The phlorotannin concentration of different species of *Sargassum* was highly variable with concentrations ranging from 1.4 to 7.3 phlorotannin % Dry Mass (Figure 29). The highest phlorotannin concentration in *S. horneri* was significantly higher than the concentration in other species (ANOVA df=3, F=77.7, p<0.001; Tukey's multiple comparisons test) and approximately five times higher than *S. agardhianum*, the species with the lowest concentration. *S. muticum* and *S. agardhianum* had significantly similar concentrations to one another, only differing by 0.02 %; these two species were significantly higher than *S. agardhianum* (Tukey's multiple comparisons test). All phlorotannin levels were mostly similar to previously published concentrations for *Sargassums* as well as for the giant kelp, *Macrocystsis pyrifera*. Levels of phlorotannins in *Macrocystis* were the standard used in the experiment to ensure that methods were properly conducted as the species exhibits minimal variability in concentrations and is well documented (Table 5). Phlorotannin concentrations for *S. muticum* in this study were lower than previously observed, although this study found high variability.

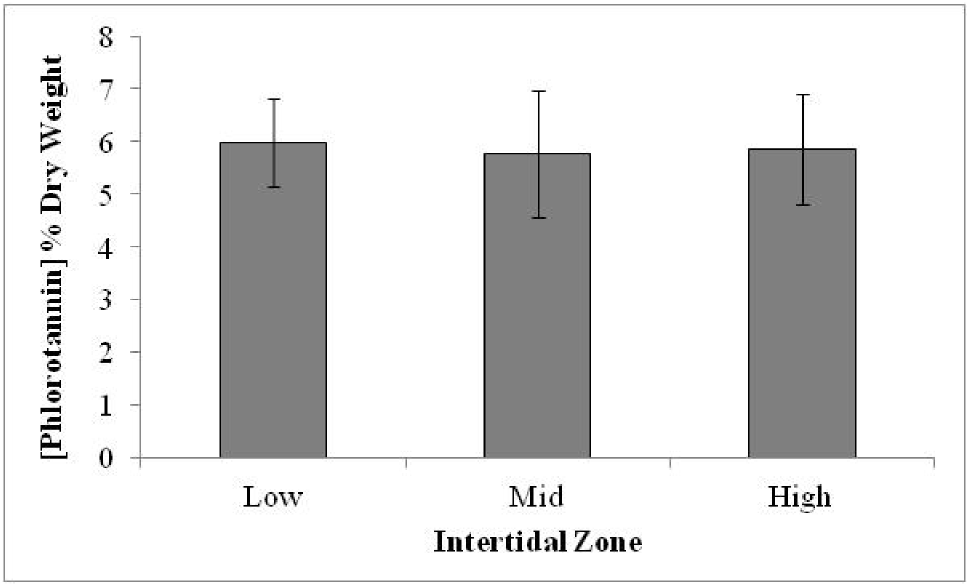

Figure 28. Mean (± SE) phlorotannin concentration of *Sargassum muticum* collected from Corona Del Mar in the low, mid and high intertidal zones.

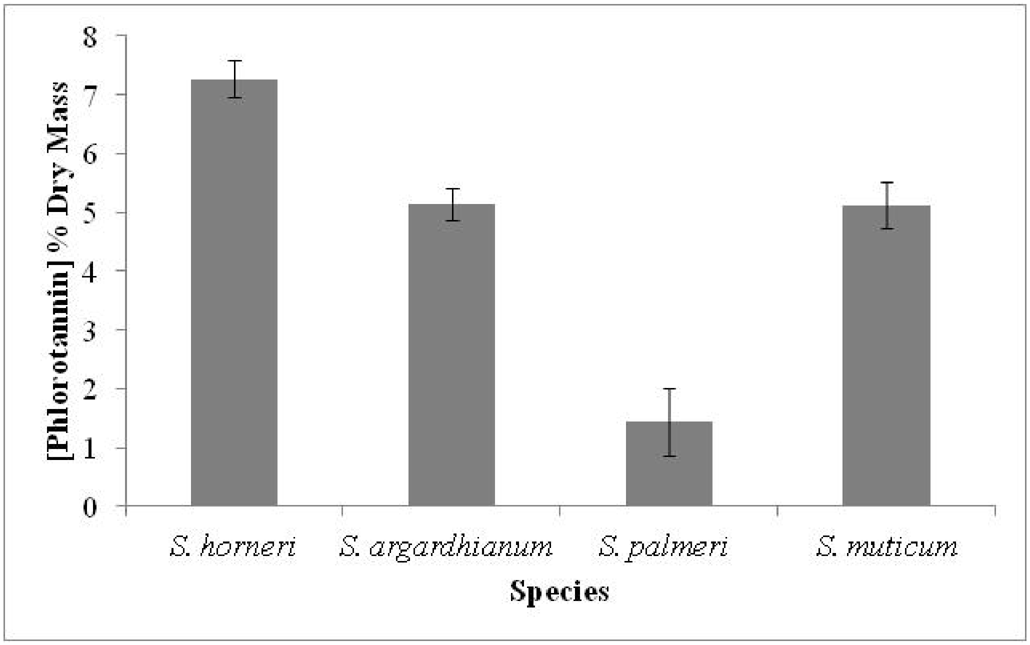

Figure 29. Mean (± SE) phlorotannin concentration of *Sargassum* species collected from Catalina Island.

Table 5. Comparison of phlorotannin concentrations of brown algae from various literature sources.

Study	Species	Phlorotannin % Dry Mass
Order Fucales:		
Connan et al. 2006	*Ascophyllum nodosum*	~5-7.0
Connan et al. 2006	*Bifurcaria bifurcata*	~3-4.3
Steinberg 1985	*Cystoseira osmundacea*	4.40
Van Alstne and Paul 1990	*Fucus distichus*	5.40
Steinberg 1985	*Fucus distichus*	4.40
White 2003	*Fucus distichus*	~5.7-6.2
Connan et al. 2006	*Fucus serratus*	~3-5.0
Connan et al. 2006	*Fucus spiralis*	~3-5.0
Connan et al. 2006	*Fucus vesiculosus*	~4-8.0
Steinberg 1985	*Halidrys dioica*	12.5
Van Alstyne et al. 1999a	*Hesperophycus harveyanus*	1.1
Connan et al. 2006	*Himanthalia elongata*	~1-5
Connan et al. 2006	*Pelvetia canaliculata*	~3-4.5
Van Alstyne and Paul 1990	*Pelvitiopsis limitata*	11.1
Steinberg 1985	*Pelvitiopsis limitata*	4.9
This study	*Sargassum argardhianum*	5.1
Nakai et al. 2006	*Sargassum horneri*	8.2
This study	*Sargassum horneri*	7.3
Steinberg 1986	*Sargassum muticum*	3.8
Le Lann et al. 2008	*Sargassum muticum*	5.8
This study	*Sargassum muticum*	5.1
Steinberg 1985	*Sargassum muticum*	3.8
White 2003	*Sargassum muticum*	~0.5
Van Alstyne et al. 1999a	*Sargassum palmeri*	1.3
This study	*Sargassum palmeri*	1.4
Van Alstyne et al. 1999b	*Silvetia compressa*	6.0
Order Laminariales:		
Steinberg 1985	*Agarum fimbriatum*	4.1
Van Alstyne and Paul 1990	*Alaria marginata*	1.4
Steinberg 1985	*Alaria marginata*	0.4
White 2003	*Alaria marginata*	~0.5-1.5
Van Alstyne and Paul 1990	*Costaria costata*	0.7
Steinberg 1985	*Costaria costata*	0.3
Van Alstyne and Paul 1990	*Egregia menziesii*	0.3
Steinberg 1985	*Egregia menziesii*	1.0
White 2003	*Egregia menziesii*	~0.3-1.5
Van Alstyne and Paul 1990	*Hedophyllum sessile*	2.0
Van Alstyne and Paul 1990	*Laminaria dentigera*	0.7
Steinberg 1985	*Laminaria dentigera*	0.5
Connan et al. 2006	*Laminaria dentigera*	~0.2
Van Alstyne et al. 1999b	*Macrocystis pyrifera*	1.2
This study	*Macrocystis pyrifera*	1.4
Van Alstyne and Paul 1990	*Nereocystis luetkeana*	0.6
Steinberg 1985	*Nereocystis luetkeana*	0.4
Van Alstyne and Paul 1990	*Postelsia palmaeformis*	0.5
Steinberg 1985	*Postelsia palmaeformis*	1.7

3.15. Impacts of herbivorous urchins.

Examination of the relationship between urchin numbers in haphazardly selected tidepools and the cover (%) of *Sargassum* or the number of *Sargassum* holdfasts in those pools exhibited some patterns (Figure 30), with especially strong patterns of *Sargassum* absence when urchin numbers were high. Equally, cover and holdfast numbers of *Sargassum* were high when urchins were absent, with exception of one tidepool. However, the relationship is complex in that there are a large number of tidepools without urchins and little or no *Sargassum* present.

In general, removal of *Sargassum* had little long-term impact on *Sargassum* cover but there was a weak pattern that indicated urchins had an impact. The trajectory of *Sargassum* cover in plots and in the entire pool over the 10-month period (Figure 31) varied significantly among removal treatments, time, and interaction terms, as well as change in urchin densities (per m^2) over time (Repeated Measures ANCOVA):

	Sargassum Cover Plot			Sargassum Cover Pool			Sargassum Holdfast Number Plot			
Factor	df	F	p-value	df	F	p-value	df	F	p-value	
Urchin density (ANCOVA)	1	4.69	**0.032**	1	6.62	**0.011**	1	0.03	0.863	
Urchin Treatment (UT)	1	0	0.998	1	0.12	0.736	1	0.17	0.684	*
Removal Treatment (RT)	1	24.83	**<0.001**	1	21.83	**<0.001**	1	7.00	**0.018**	*
Time	11	16.73	**<0.001**	11	17.60	**<0.001**	11	9.65	**<0.001**	
UT*RT	1	0.08	0.783	1	0.01	0.934	1	0.17	0.690	*
UT*Time	11	4.27	**<0.001**	11	3.57	**<0.001**	11	0.90	0.538	
RT*Time	11	19.24	**<0.001**	11	21.32	**<0.001**	11	2.66	**0.004**	
UT*RT*Time	11	0.76	0.682	11	0.75	0.686	11	0.65	0.787	
Plot (UT RT)	16	19.78	**<0.001**	16	20.41	**<0.001**	16	44.09	**<0.001**	
*=F stat not exact										

The number of *Sargassum* holdfasts (approximate) exhibited somewhat similar patterns, although the urchin density co-variate was not significant.

In control plots, *Sargassum* cover in both plots and the entire tidepool exhibited a natural decline in cover in the summer time and recovered in late fall (Figure 31), much like seasonal variation previously observed in the prior experiment (see Figure 19). Urchin transplants resulted in a larger decline in *Sargassum* cover initially in spring and summer with a slower recovery in fall. Removal plots exhibited rapid recovery through late fall, a decline in spring, and then continued recovery to control plot levels by mid fall. Similar patterns were observed in the removal + transplant plots, but at a lower level.

For *Sargassum* holdfast number, there was a general decrease in both controls and urchin transplant plots in spring, followed by a steady increase in summer, and a stabilization in fall (Figure 31). This data did not match cover data well; this may be due to *Sargassum* reproduction in the spring whereby new individuals recruit in summer which contribute little to percent cover while adults that contribute the most to percent cover were dying back post-reproduction. Both removal treatments exhibited a steady increase in *Sargassum* holdfast numbers over time.

Urchin densities in control plots were stable throughout the experiment (Figure 32) while in plots where urchins were transplanted, there was a steady decline over time. Urchin densities remained significantly different among treatment types (ANOVA analyses on a monthly basis; urchin treatment $p<0.05$) until the last sampling in December 2013 when urchin densities were the same across all treatments (ANOVA urchin treatment $p=0.060$).

At the end of the 10-month long experiment, *Sargassum* cover in plots and pools, as well as *Sargassum* holdfast number, were similar among urchin and removal treatments (Figure 33), although a block effect was found for all three data sets:

	Sargassum Cover Plot			Sargassum Cover Pool			Sargassum Holdfast Number Plot		
Factor	df	F	p-value	df	F	p-value	df	F	p-value
Urchin Treatment (UT)	1	2.01	0.182	1	0.65	0.435	1	0.80	0.388
Removal Treatment (RT)	1	2.01	0.182	1	0.65	0.435	1	1.58	0.233
UT*RT	1	2.99	0.110	1	1.07	0.321	1	2.38	0.149
Blocks (Random)	4	4.46	**0.019**	4	3.43	**0.043**	4	4.16	**0.024**

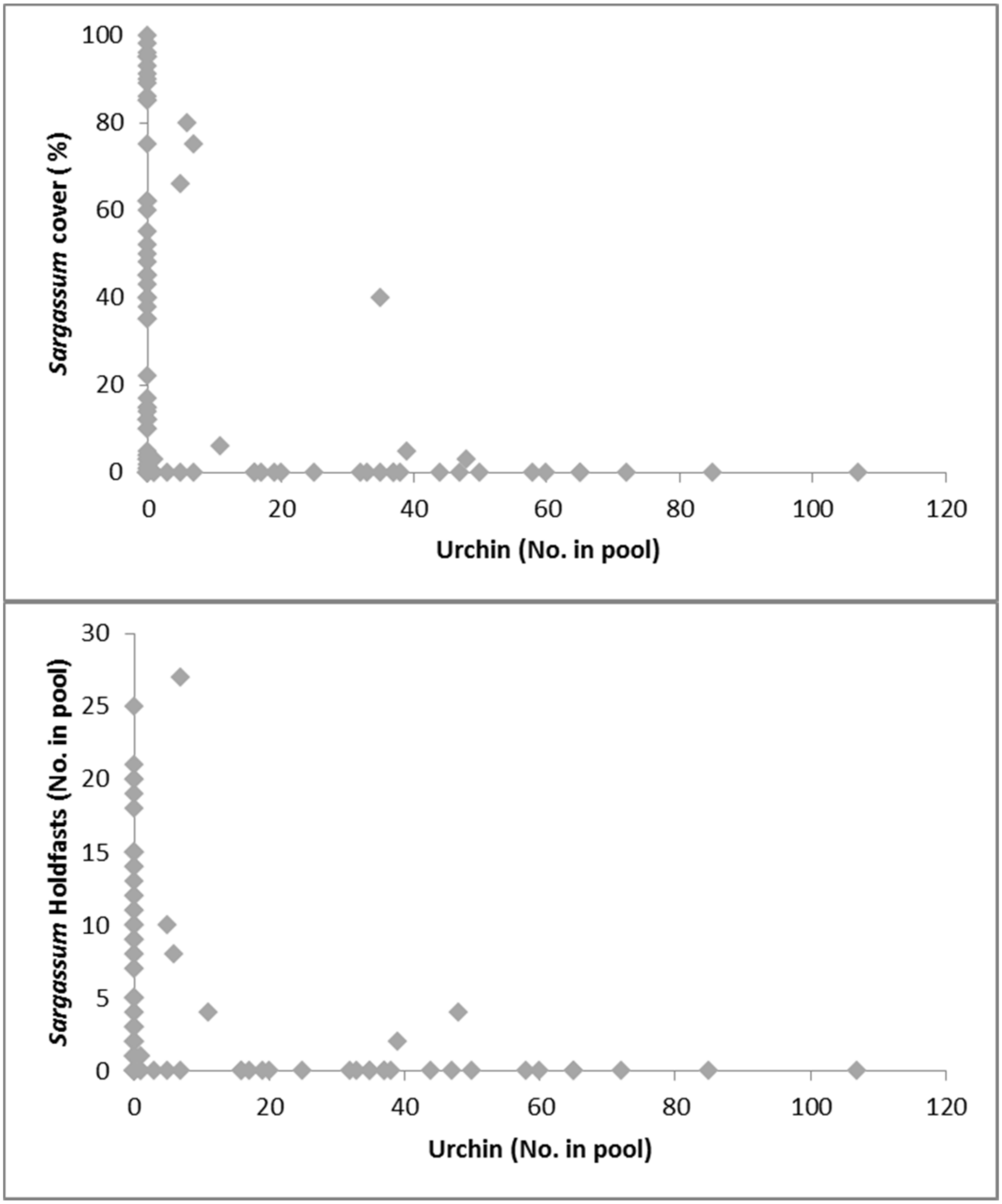

Figure 30. The relationship between urchin numbers in pools and *Sargassum* cover (upper figure) or *Sargassum* holdfast counts (lower figure).

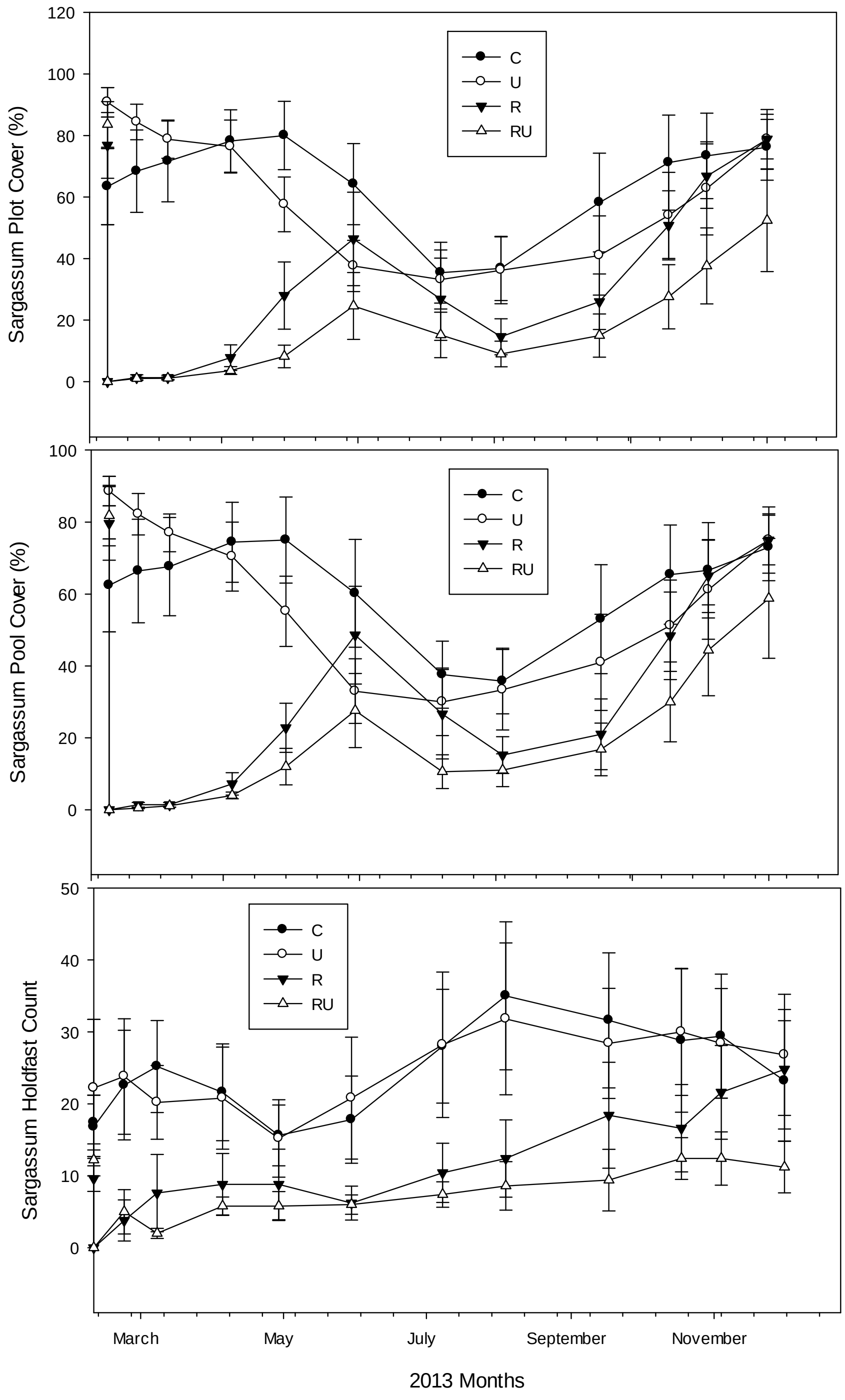

Figure 31. Mean *Sargassum* cover in plots and pools and *Sargassum* holdfast counts (+/- SE) for the four treatments (C=*Sargassum* Control, U=Urchin Transplant, R=*Sargassum* Removal, RU=*Sargassum* Removal + Urchin Transplant) over the 10 month experimental period in 2013.

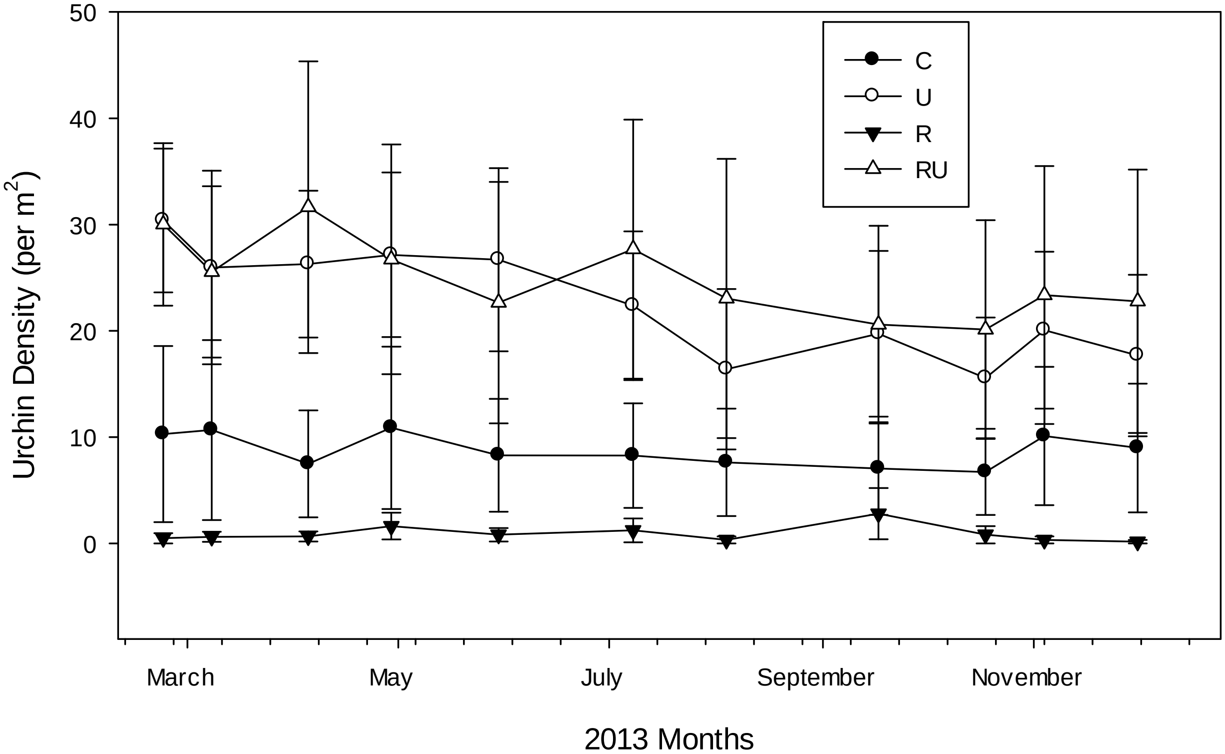

Figure 32. Mean urchin density (per m^2; +/- SE) for the four treatments (C=*Sargassum* Control, U=Urchin Transplant, R=*Sargassum* Removal, RU=*Sargassum* Removal + Urchin Transplant) over the 10 month experimental period in 2013.

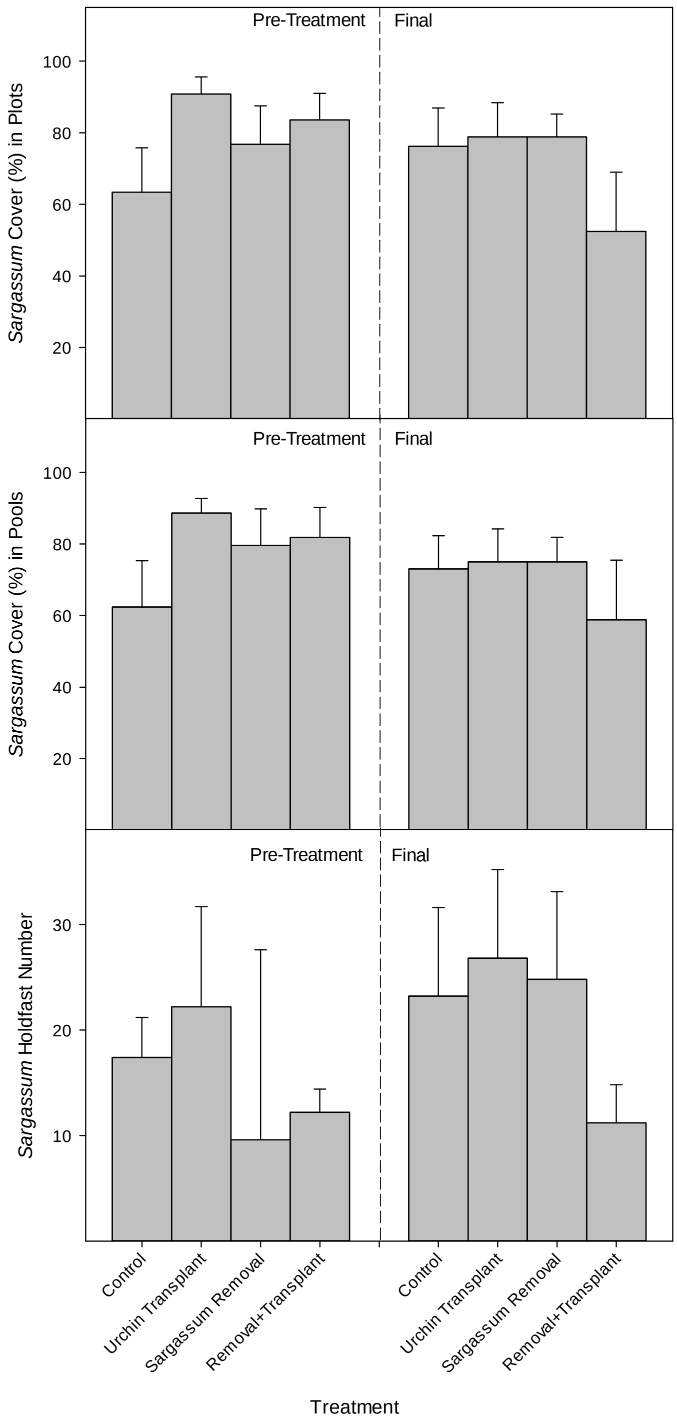

Figure 33. Mean cover (+/- SE) of *Sargassum* in plots and tidepools and the holdfast number in plots (+/- SE) prior to application of treatments and at the end of the 10-month long study for each of the four treatments.

3.16. Large Tidepool Preliminary Investigations.

In the large upper intertidal tidepool (~250 m^2) at Little Corona del Mar, there was a weak positive relationship between *Sargassum* cover and sand entrapment (Figure 34) in both April and November 2012. The relationship between *Sargassum* holdfast number and sand entrapment was also weak for November but moderate for April (Figure 34). In general, sand cover increased as *Sargassum* cover or holdfast number increased.

Fourteen 1 m^2 plots were harvested within the large tidepool. On average, there were 106 holdfasts (+/- 19.6 SE) per m^2 which took an average of 45 minutes (+/- 7.7) per plot to clear of *Sargassum* (~30 seconds per holdfast). This was faster than time spent on individual plots which, on average, took 1.15 hours per m^2. Scaled up for the entire 250 m^2 plot, it is estimated that it would take one individual ~190 hours to clear the large plot.

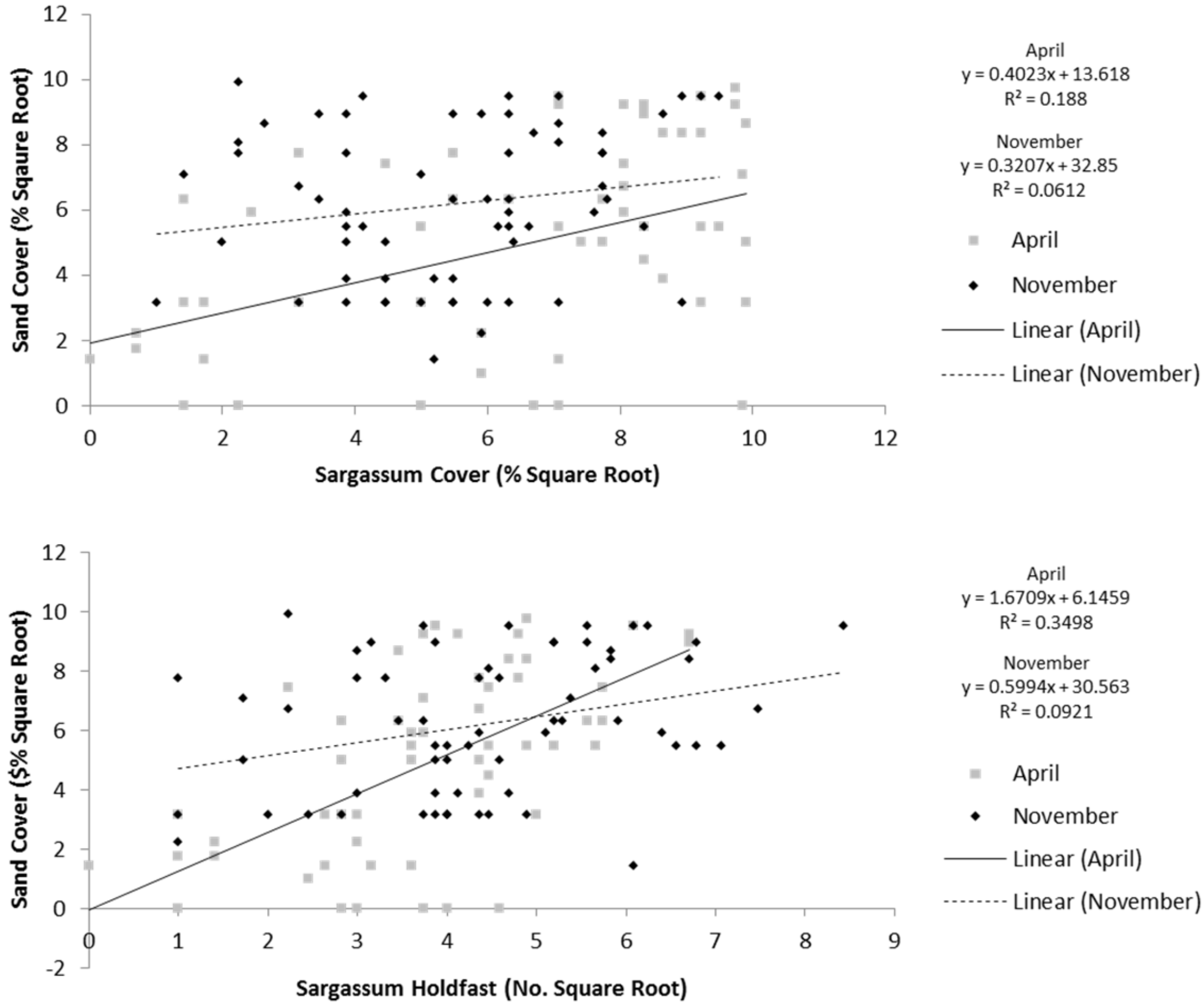

Figure 34. Relationship between sand cover and *Sargassum* cover or *Sargassum* holdfast number (square root transformed data) in April 2012 and November 2012.

3.2. *Caulacanthus ustulatus*

3.21. Impacts on community structure.

Univariate analyses of taxa of the four data sets, all cover, macrophyte presence, macroinvertebrate counts, and subplot macro- and meiofauna counts, yielded few significant results. For cover data for the high intertidal zone, *Caulacanthus* and total biotic cover was significantly higher in non-native *Caulacanthus* plots while bare rock cover was significantly higher in native plots (Table 6). In the middle intertidal zone, *Caulacanthus* cover was significantly higher in the non-native plots while the red algae *Ceramium* and *Corallina* were higher in the native plots. The frequency of presence of the red alga *Gelidium coulteri* and the green alga *Ulva californica* was higher in non-native plots in the high zone while two filamentous like red algal species, *Centrocerus* and *Ceramium*, were more common in native plots in the middle intertidal zone (Table 7). For macroinvertebrate counts, the barnacle *Chthamalus* spp. and all barnacles combined were significantly higher in native plots in the high zone while no differences were observed in the mid zone (Table 8). In subplots, Cirripeds were significantly more common in the native plots while isopods were more common in non-native plots in the high zone. In the middle zone, gastropods, amphipods, and pycnogonids were more common in the native turf samples (Table 9).

Species richness calculated from the four data sets was significantly higher in the non-native plots in the high intertidal zone for cover data, seaweed presence, and macro/meiofauna data while no difference was observed in macroinvertebrate count richness (Figure 35; Table 10). In the middle intertidal zone, richness was similar for all data sets. For species diversity (H' index), significant differences were only observed in the high intertidal zone for subplot macro/meiofauna data where H' was higher in the non-native plots (Figure 36; Table 10).

A series of multidimensional scaling plots were created to depict differences in community assemblages among native non-*Caulacanthus* plots and non-native *Caulacanthus* plots in the two zones for all four data sets (Figures 37-40). Two Factor ANOSIM analyses (Patch [native vs non-native] and zone [high vs mid] as fixed factors) reveal significant differences between zones and between patches for each data type, except patch for macroinvertebrate abundance (Table 11). When examining the zones separately, there was a clear pattern of significant differences between patches for all data sets in the high zone but no differences in assemblages in the middle intertidal zone (Table 11).

The species contributing most to the dissimilarity between treatments for the upper and middle intertidal zones were highly variable between zones for each data set (SIMPER; Table 12). In general, the upper intertidal was driven by more barnacles (*Chthamalus*), rock, limpets, and encrusting algae in the native patches and by more fleshy seaweeds and small meiofauna, such as ostracods and isopods, in the non-native patches. In the middle intertidal zone, fleshy seaweeds were more common in the native patches while gastropods, and sipunculids were more common in non-native patches.

No measurable sediment was found in native patches in the upper intertidal zone compared to ~230 $cm^3\ m^{-2}$ (+/- 29) in non-native patches (Figure 41). In contrast, native turf patches in the middle intertidal zone had more sediment accumulation (~560 $cm^3\ m^{-2}$ +/- 254) than non-native *Caulacanthus* turfs (~368 $cm^3\ m^{-2}$ +/- 124). Because of this pattern, two-factor ANOVA analyses revealed a significant interaction term (4^{th} root transformed, presence of *Caulacanthus* df=1, F=27.3, p<0.001; site df=4, F=54.7, p<0.001; S X C df=4, F=45.8, p<0.001). Analyzing the zones separately reveal that sediment accumulation in non-native plots in the high zone is significantly higher than native plots (T-Test, df=13, T=-16.0, p<0.001) while no difference was observed in the middle intertidal zone (T-Test, df=16, T=0.91, p=0.377).

Table 6. Mean percent cover (+/- SE) of abiotic, seaweeds, and macroinvertebrates in native and non-native plots in the high and middle intertidal zones. Included are T-Test results comparing native and non-native patches for each zone.

	High Zone						Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value		Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Abiotic:											
Rock	58.9	7.1	20.25	3.3	**0.000**		5.2	1.4	6.4	0.8	0.434
Sand	0.6	0.4	2.15	0.9	0.312		0.7	0.3	2.3	0.8	0.175
Seaweeds:											
Caulacanthus ustulatus	2.1	1.2	62.4	4.1	**0.000**		4.3	1.6	58.3	5.0	**0.000**
Centrocera clavulatum							2.4	0.9	1.3	1.0	0.500
Ceramium spp.							0.7	0.4	0.0	0.0	**0.035**
Chaetomorpha linum	0.0	0.0	0.05	0.1	0.453						
Chondracanthus canaliculatus	0.0	0.0	0.15	0.1	0.453		3.5	2.4	2.0	1.3	0.535
Colpomenia sinuosa							0.2	0.1	0.1	0.1	0.453
Corallina pinnatifolia	0.2	0.2	10.8	6.8	0.150		78.3	6.1	40.5	6.3	**0.002**
Crustose Coralline	2.0	0.9	3	2.0	0.823		2.7	0.8	3.2	1.2	0.792
Gelidium pusillum	0.0	0.0	8.2	3.2	0.058		13.7	13.3	2.3	0.8	0.234
Laurencia pacifica	0.0	0.0	0.05	0.1	0.453						
Lithothrix aspergillum							1.7	1.7	0.0	0.0	0.163
Lomentaria hakodotensis							0.3	0.3	0.4	0.3	0.862
Osmundea sinicola							0.2	0.2	0.1	0.1	0.781
Petrospongium rugosom	0.1	0.1	2	1.2	0.276		0.1	0.1	0.1	0.1	1.000
Polysiphonia spp.	1.0	1.0	0	0.0	0.220		0.5	0.5	0.6	0.6	0.892
Psuedolithoderma nigra	10.0	10.0	1.6	0.8	0.320		2.7	1.8	3.6	1.5	0.714
Pterocadiella capilacea							0.5	0.5	0.1	0.1	0.267
Ralfsia	2.9	1.8	2.2	0.8	0.933		1.8	1.7	1.1	0.6	0.674
Scytosiphon lometaria	0.2	0.2	0.55	0.4	0.435						
Ulva californica	0.0	0.0	1.95	0.8	0.059		3.0	0.5	3.9	0.5	0.279

Table 6 Continued.

	High Zone					Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Invertebrates:										
Acmea mitra						0.1	0.1	0.0	0.0	0.163
Agnathostoma eiseni						0.0	0.0	0.0	0.0	0.496
Anthopleura spp.	2.1	1.5	1	0.6	0.582	0.5	0.2	0.5	0.3	0.935
Balanus glandula	0.4	0.2	1.1	1.1	0.594	0.0	0.0	0.1	0.1	0.317
Chlorostoma auriotincta						0.0	0.0	0.0	0.0	0.496
Chlorostoma funebralis	0.4	0.4	0.7	0.5	0.445					
Chthamalus spp	12.1	5.0	0.8	0.4	**0.016**	0.4	0.2	0.4	0.2	1.000
Cyanoplax hartwegii	0.0	0.0	0.15	0.1	0.453					
Diptera	0.0	0.0	0.05	0.1	0.453					
Fisurella volcano						0.2	0.1	0.1	0.1	0.453
Littorina spp.	1.8	1.1	0.65	0.4	0.357					
Lottia digitalis	0.1	0.1	0	0.0	0.220					
Lottia limatula						0.2	0.1	0.2	0.1	0.793
Lottia scabra/conus	0.9	0.2	0.95	0.2	0.678	0.5	0.2	0.5	0.1	1.000
Lottia strigitella	2.0	0.8	0.85	0.1	0.090	0.2	0.1	0.3	0.1	0.604
Mytilus californianus	0.4	0.2	0.1	0.1	0.127	0.0	0.0	0.1	0.1	0.317
Nuttalina spp	0.3	0.2	0.45	0.2	0.487	0.5	0.1	0.4	0.1	0.674
Pachygrapsus crassipes	0.0	0.0	0.05	0.1	0.453	0.1	0.1	0.0	0.0	0.621
Pagurus samuelis	0.0	0.0	0.35	0.2	0.453	0.3	0.2	0.2	0.2	0.646
Phragmatopoma californica						0.2	0.2	0.1	0.1	0.621
Serpulorbis squamigerus						0.1	0.1	0.2	0.2	0.739
Spirobranchus spp.						0.2	0.1	0.5	0.2	0.423
Sprirorbis spp.						0.1	0.1	0.0	0.0	0.163
Stenoplex spp.										
Strongylocentrotus purpuratus						0.3	0.3	0.0	0.0	0.163
Tetraclita rubescens	0.0	0.0	0.1	0.1	0.453					
Unidentified annelid						0.1	0.1	0.0	0.0	0.163
Unidentified clam						0.0	0.0	0.0	0.0	0.496
Total biotic	39.0	7.2	100.25	7.0	**0.000**	120.3	14.1	121.3	8.3	0.947

Table 7. Mean frequency of presence (+/- SE) of macroalgae in native and non-native plots in the high and middle intertidal zones. Included are T-Test results comparing native and non-native patches for each zone.

	High Zone						Middle				
	Native	Native SE	Non-Native	Non-Native	T-test		Native	Native SE	Non-Native	Non-Native	T-test
Caulacanthus ustulatus	0.6	0.2	1	0.0	0.057		0.8	0.2	1.0	0.0	0.163
Centrocera clavulatum							0.8	0.2	0.2	0.1	**0.004**
Ceramium spp.							0.3	0.2	0.0	0.0	**0.035**
Chaetomorpha linum	0.0	0.0	0.1	0.1	0.453						
Chondracanthus canaliculatus	0.0	0.0	0.2	0.1	0.453		0.7	0.2	0.4	0.1	0.346
Colpomenia sinuosa							0.3	0.2	0.2	0.1	0.453
Corallina pinnatifolia	0.2	0.2	0.7	0.2	0.059		1.0	0.0	1.0	0.0	1.000
Crustose Coralline	0.6	0.2	0.4	0.2	0.241		0.8	0.2	0.7	0.1	0.486
Gelidium pusillum	0.0	0.0	0.7	0.2	**0.004**		0.3	0.2	0.5	0.2	0.531
Laurencia pacifica	0.0	0.0	0.1	0.1	0.453						
Lithothrix aspergillum							0.2	0.2	0.0	0.0	0.163
Lomentaria hakodotensis							0.2	0.2	0.2	0.1	1.000
Osmundea sinicola							0.2	0.2	0.3	0.1	0.709
Petrospongium rugosom	0.2	0.2	0.4	0.2	0.546		0.2	0.2	0.2	0.1	1.000
Polysiphonia spp.	0.2	0.2	0	0.0	0.220		0.2	0.2	0.2	0.1	1.000
Psuedolithoderma nigra	0.2	0.2	0.4	0.2	0.546		0.3	0.2	0.5	0.2	0.531
Pterocadiella capilacea							0.2	0.2	0.1	0.1	0.621
Ralfsia	0.4	0.2	0.5	0.2	0.471		0.3	0.2	0.3	0.1	1.000
Scytosiphon lometaria	0.2	0.2	0.2	0.1	0.851						
Ulva californica	0.0	0.0	0.7	0.2	**0.000**		1.0	0.0	1.0	0.0	1.000

Table 8. Mean macroinvertebrate counts (+/- SE) in native and non-native plots in the high and middle intertidal zones. Included are T-Test results comparing native and non-native patches for each zone.

	High Zone					Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Acmea mitra						0.2	0.2	0.0	0.0	0.163
Agnathostoma eiseni						0.0	0.0	0.3	0.3	0.496
Anthopleura spp.	3.8	2.9	0.9	0.4	0.180	0.8	0.3	0.5	0.2	0.408
Balanus glandula	1.0	0.4	3.4	3.4	0.633	0.0	0.0	0.6	0.5	0.428
Chlorostoma auriotincta						0.0	0.0	0.1	0.1	0.496
Chlorostoma funebralis	0.2	0.2	2.2	1.7	0.428					
Chthamalus spp	235.6	123.0	16.3	9.0	**0.022**	9.8	4.5	9.9	5.2	0.992
Cyanoplax hartwegii	0.0	0.0	0.3	0.2	0.347					
Diptera	0.0	0.0	0.1	0.1	0.500					
Fisurella volcano	0.0	0.0	0	0.0		0.3	0.2	0.3	0.2	0.781
Littorina spp.	28.6	19.4	6.6	4.4	0.157					
Lottia digitalis	0.4	0.4	0	0.0	0.165					
Lottia limatula	0.0	0.0	0	0.0		0.5	0.3	0.4	0.3	0.852
Lottia pelta	0.0	0.0	0	0.0						
Lottia scabra/conus	6.0	1.6	6.3	2.5	0.938	4.7	2.2	7.6	2.1	0.401
Lottia strigitella	10.8	4.5	5.8	1.7	0.228	0.3	0.2	1.3	0.6	0.275
Mite	0.2	0.2	0	0.0	0.165					
Mytilus californianus	2.4	1.6	0.3	0.2	0.086	0.0	0.0	0.2	0.2	0.496
Nuttalina spp	0.4	0.2	0.4	0.2	1.000	2.3	0.7	2.0	0.7	0.768
Pachygrapsus crassipes	0.0	0.0	0.1	0.1	0.500	0.2	0.2	0.1	0.1	0.621
Pagurus samuelis	0.0	0.0	1.2	0.9	0.380	0.7	0.3	0.3	0.3	0.453
Phragmatopoma californica						0.2	0.2	0.1	0.1	0.621
Serpulorbis squamigerus						0.5	0.5	0.1	0.1	0.267
Spirobranchus spp.						0.3	0.2	2.9	2.0	0.390
Sprirorbis spp.						3.2	3.2	0.0	0.0	0.163
Strongylocentrotus purpuratus						0.2	0.2	0.0	0.0	0.163
Tetraclita rubescens	0.0	0.0	0.3	0.3	0.500	0.0	0.0	0.0	0.0	
Unidentified annelid						0.2	0.2	0.0	0.0	0.163
All Limpets	17.2	4.0	12.1	3.8	0.416	6.0	2.2	9.6	2.2	0.311
All Barnacles	236.6	123.3	20	12.5	**0.025**	9.8	4.5	10.5	5.7	0.940

Table 9. Mean counts of macro- and meiofauna (+/- SE) in subplots in native and non-native plots in the high and middle intertidal zones. Included are T-Test results comparing native and non-native patches for each zone.

	High Zone					Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Molluscs Bivalvia	0.0	0.0	1.2	0.5	0.090	1.8	1.3	0.7	0.4	0.266
Molluscs Gastropods	2.8	1.0	2.6	1.4	0.932	75.3	27.0	24.3	6.7	**0.026**
Annelids Polychaets	0.0	0.0	0.1	0.1	0.453	0.3	0.3	0.1	0.1	0.346
Arthropods Cirripedia	11.0	4.4	0	0.0	**0.008**					
Arthropods Isopods	0.0	0.0	1.8	0.5	**0.014**	0.8	0.3	3.3	2.1	0.427
Arthropods Amphipods						4.2	1.5	0.9	0.4	**0.014**
Arthropods Copepods	0.0	0.0	0.5	0.3	0.291	0.2	0.2	1.3	0.6	0.176
Arthropods Ostracods A						0.0	0.0	0.8	0.8	0.496
Arthropods Insects	0.0	0.0	0.4	0.3	0.453	2.8	1.9	2.8	0.9	0.964
Arthropods Ostracods B	0.0	0.0	3.2	1.7	0.174	4.5	1.3	3.4	0.8	0.462
Arthropods Pycnogonid						0.3	0.2	0.0	0.0	**0.035**
Arthropods Arachnids	0.0	0.0	0.2	0.1	0.260	1.2	0.6	1.0	0.6	0.862
Foraminifera	0.0	0.0	0.1	0.1	0.453	0.5	0.2	0.2	0.1	0.153
Nematoda	0.0	0.0	0.6	0.3	0.453	2.2	1.6	0.8	0.4	0.308
Sipunculid	0.0	0.0	0.7	0.3	0.116	11.5	8.2	3.5	1.3	0.197
Cnidarian						0.0	0.0	0.1	0.1	0.496

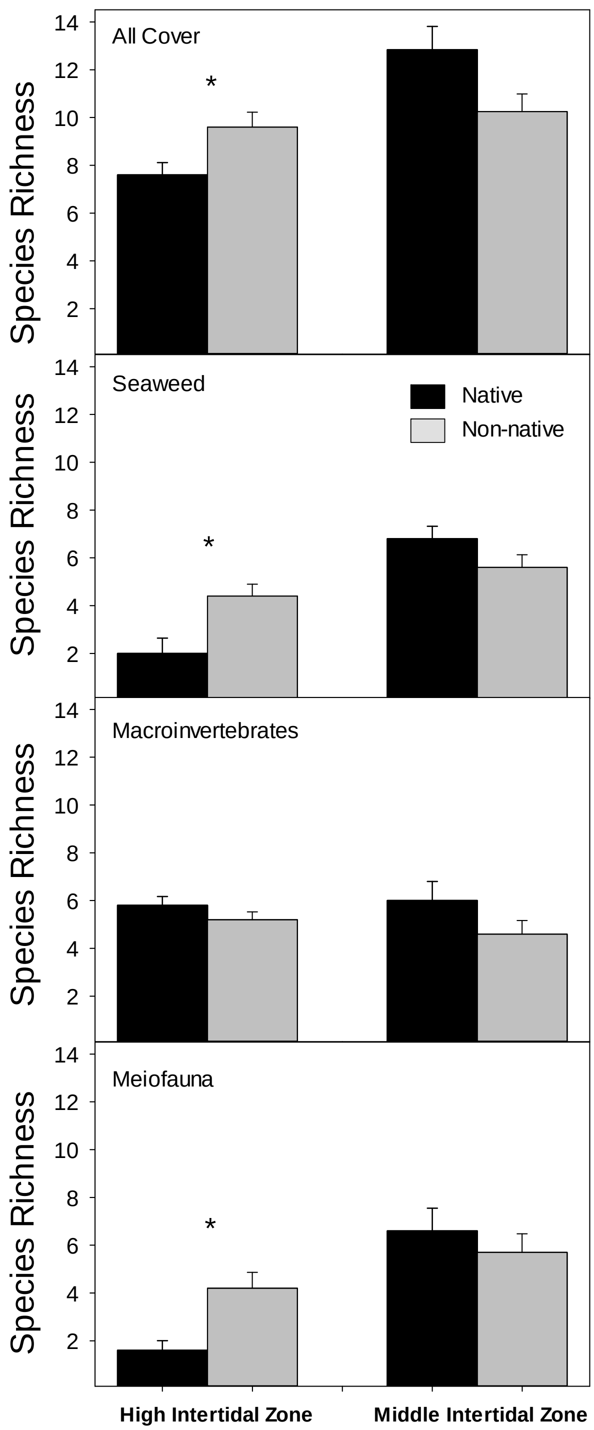

Figure 35. Mean species richness (+/- SE) for native (black bars) and non-native (gray bars) plots for the four data sets. The asterisks depict significant differences between patches within a zone (T-Test $p<0.05$).

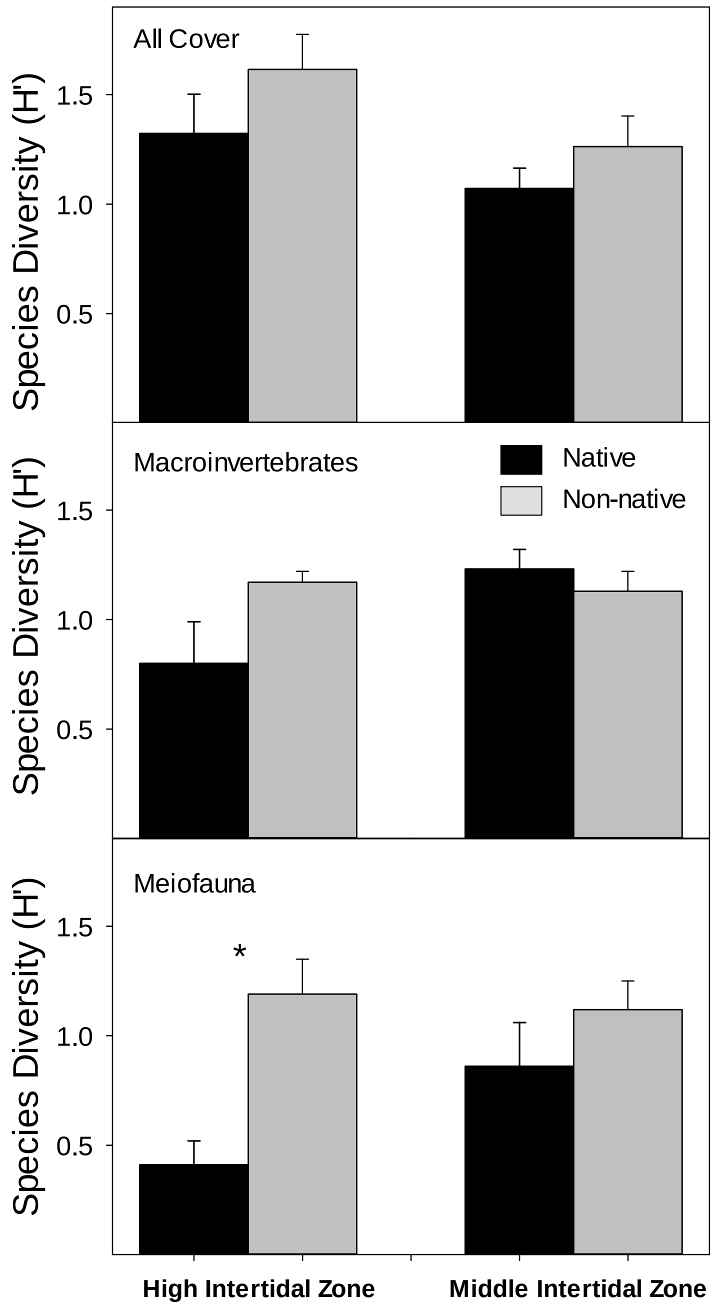

Figure 36. Mean species diversity (H’ index; +/- SE) for native (black bars) and non-native (gray bars) plots for the four data sets. The asterisk depict significant differences between patches within a zone (T-Test $p<0.05$).

Table 10. T-test results (df, T stat, and p value) for comparisons of species richness and species diversity (H’ index) between native and non-native patches for the upper and middle intertidal zone.

	T-Test			**T-Test**		
	Upper Zone			**Middle Zone**		
	df	**T**	**p value**	**df**	**T**	**p value**
All Cover Richness	12	-2.50	**0.028**	10	2.11	0.061
All Cover H'	10	-1.24	0.243	15	-1.16	0.265
Macroalgae Richness	12	-4.06	**0.002**	13	1.92	0.078
Macroinvertebrate Richness	9	1.21	0.258	9	1.24	0.247
Macroinvertebrate H'	4	-1.88	0.133	14	0.32	0.755
Meiofauna Richness	12	-3.36	**0.006**	11	1.22	0.247
Meiofauna H'	12	-3.94	**0.002**	9	-0.80	0.444

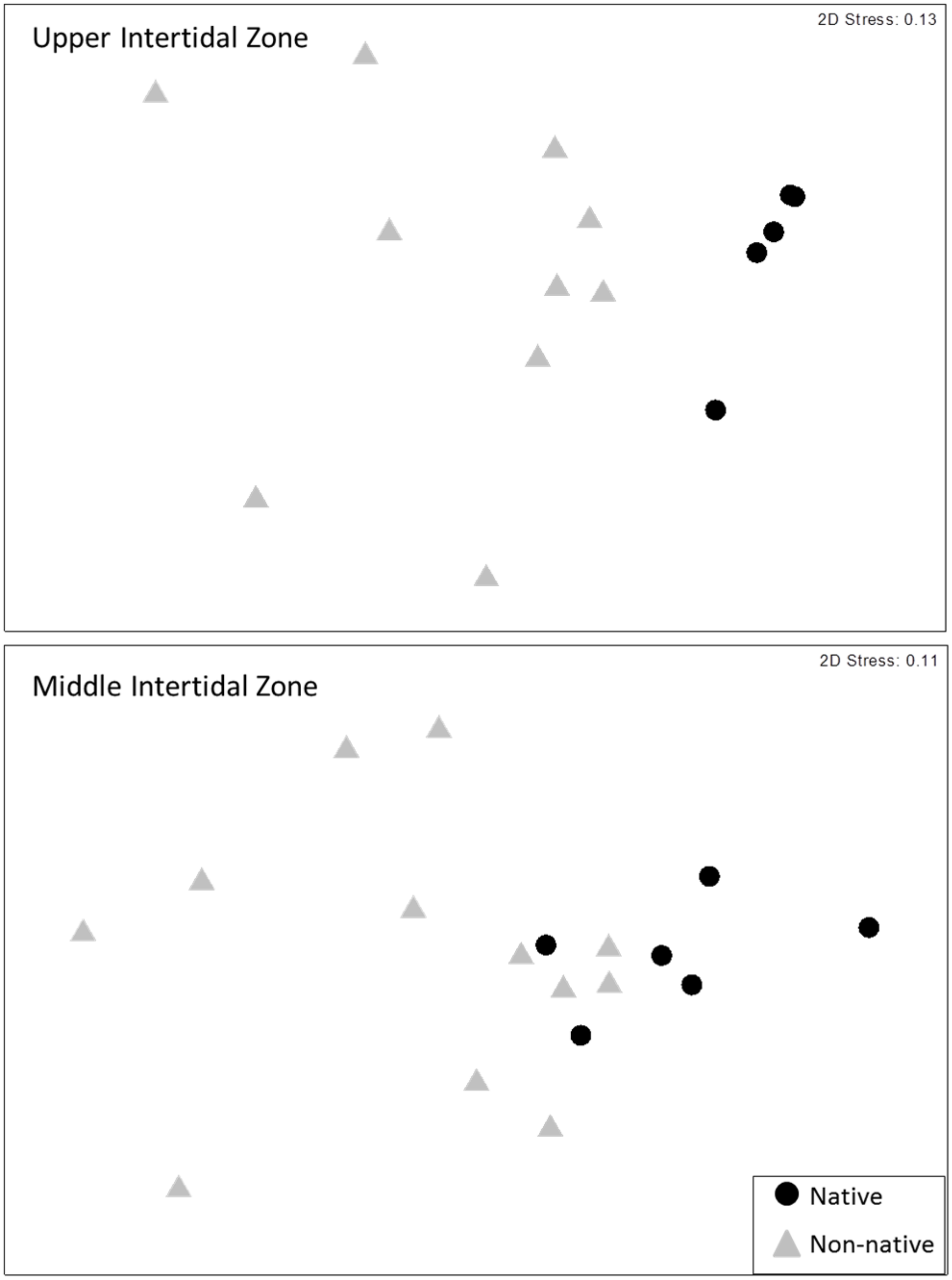

Figure 37. Multidimensional scaling plot for community assemblages using cover data in native (black circles) and non-native patches (grey triangles) in the upper and middle intertidal zones. ANSOIM results reveal significant differences between patches in the upper zone but not in the middle zone (Table 11).

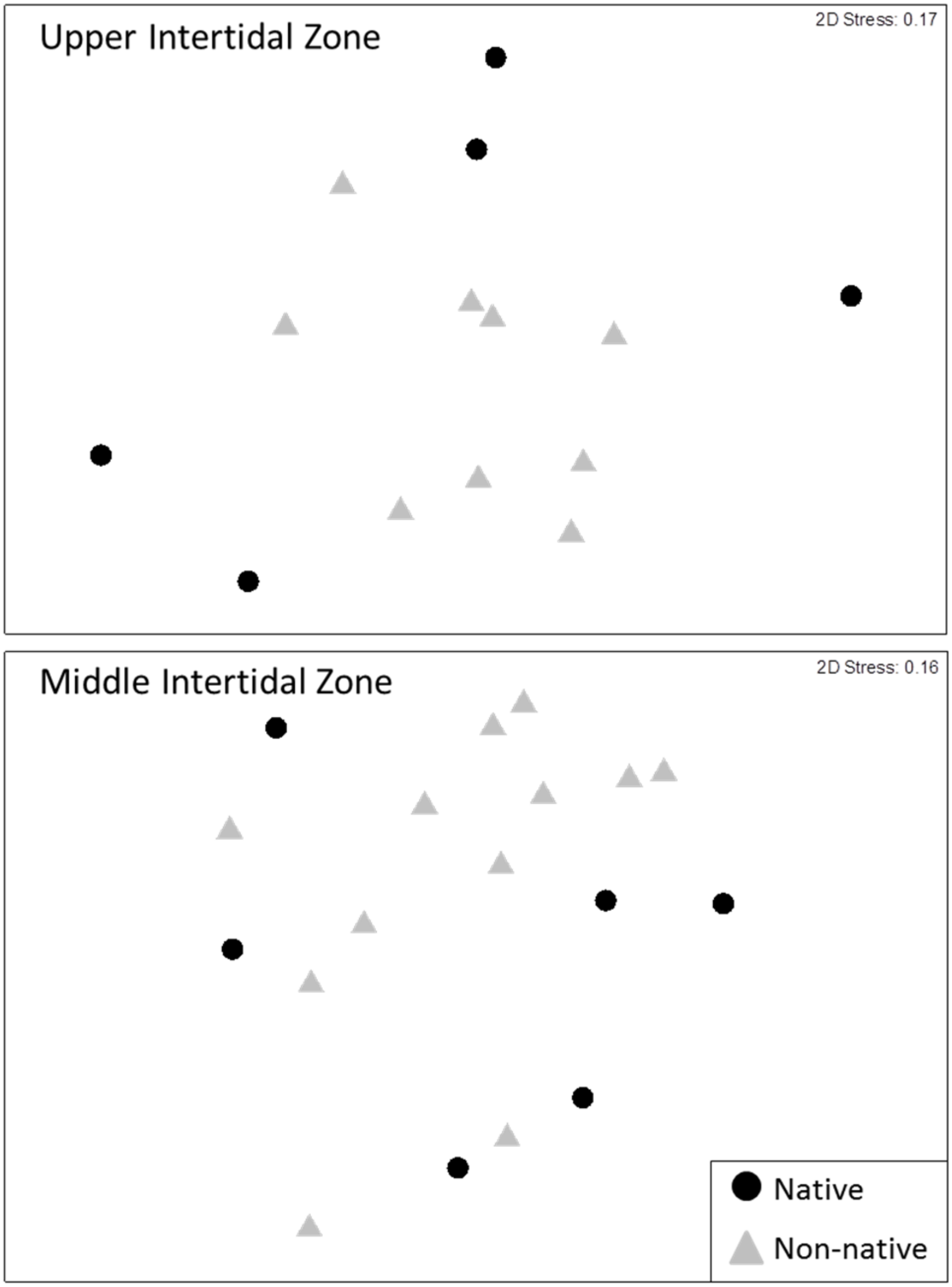

Figure 38. Multidimensional scaling plot for community assemblages using macroalgal presence in (black circles) and non-native patches (grey triangles) in the upper and middle intertidal zones. ANSOIM results reveal significant differences between patches in the upper zone but not in the middle zone (Table 11).

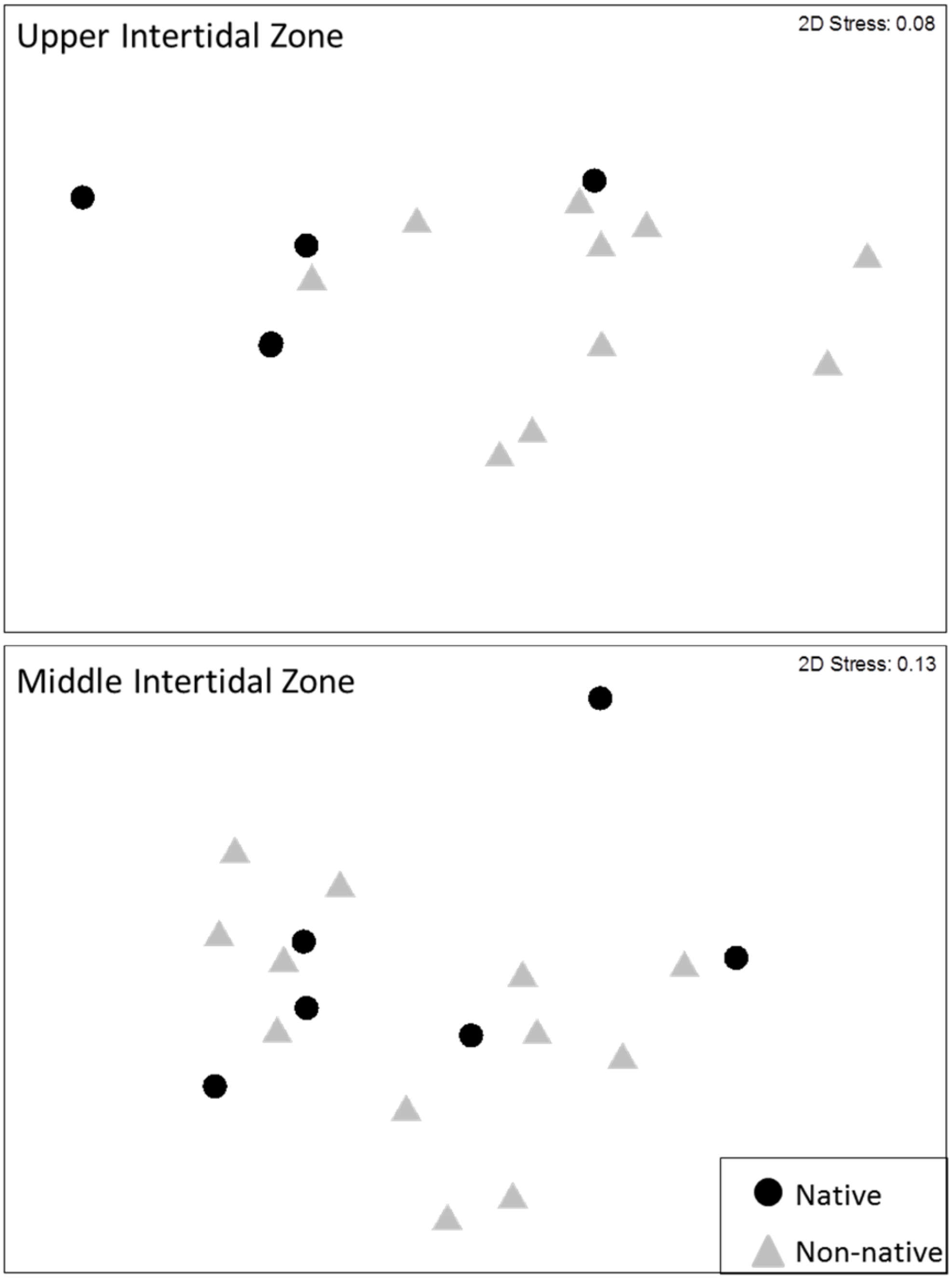

Figure 39. Multidimensional scaling plot for community assemblages using macroinvertebrate counts in native (black circles) and non-native patches (grey triangles) in the upper and middle intertidal zones. ANSOIM results reveal significant differences between patches in the upper zone but not in the middle zone (Table 11).

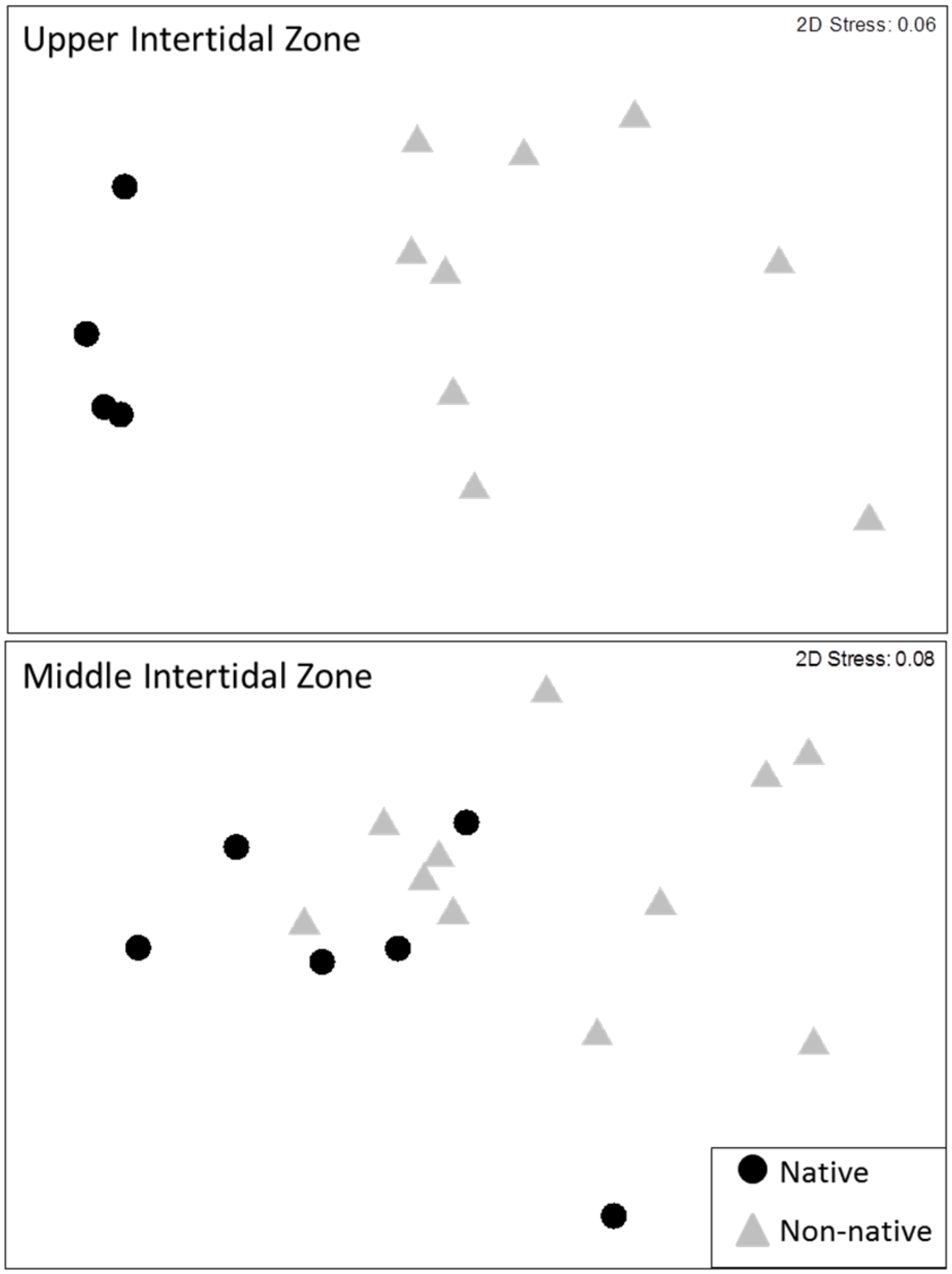

Figure 40. Multidimensional scaling plot for community assemblages using counts of macro- and meiofauna from subplots in native (black circles) and non-native patches (grey triangles) in the upper and middle intertidal zones. ANSOIM results reveal significant differences between patches in the upper zone but not in the middle zone (Table 11).

Table 11. ANOSIM results (Global R and p- value) of community assemblage comparisons. Included are results from the Two-Factor ANOSIM (Patch and zone as fixed factors) as well as the ANOSIM results for the individual tidal zones.

	Two-Factor ANOSIM Results				ANOSIM Results			
	Patch		Zone		Patch: Upper Zone		Patch: Middle Zone	
	Global R	**p value**	**Global R**	**p value**	**Global R**	**p value**	**Global R**	**p value**
All cover data (%, abiotic included, *Caulacanthus* excluded)	0.682	**0.001**	0.198	**0.024**	0.348	**0.009**	0.099	0.179
Macroalgal presence (frequency, *Caulacanthus* excluded)	0.187	**0.002**	0.152	**0.007**	0.345	**0.019**	0.093	0.165
Macroinvertebrate abundance (# per plot)	0.051	0.210	0.220	**0.003**	0.308	**0.028**	0.005	0.477
Meiofauna abundance (# per plot)	0.209	**0.027**	0.332	**0.001**	0.449	**0.006**	0.050	0.281

Table 12. SIMPER results for species contributing most to dissimilarity between native and non-native patches in the upper and middle intertidal zones for cover, macroalgal presence, macroinvertebrate counts, and macro/meiofauna abundances.

Intertidal Zone	Data Set	Species	Native	Non-native	~ Dissimilarity Contribution (%)
Upper	Cover Data	Rock	58.9 (7.1)	20.25 (3.3)	38
		Chthamalus spp	12.1 (5.0)	0.8 (0.4)	11
		Psuedolithoderma nigra	10.0 (10.0)	1.6 (0.8)	11
		Corallina pinnatifolia	0.2 (0.2)	10.8 (6.8)	8
		Gelidium spp.	0 (0.0)	8.2 (3.2)	8
	Macroalgae presence (mean frequency)	*Gelidium* spp.	0.0 (0.0)	0.7 (0.2)	14
		Ulva californica	0.0 (0.0)	0.7 (0.2)	13
		Corallina pinnatifolia	0.2 (0.2)	0.7 (0.2)	12
		Crustose Coralline	0.6 (0.2)	0.4 (0.2)	10
		Ralfsiaceae	0.4 (0.2)	0.5 (0.2)	10
		Psuedolithoderma nigra	0.2 (0.2)	0.4 (0.2)	9
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	235.6 (123.0)	16.3 (9.0)	65
		Littorina spp	28.6 (19.4)	6.6 (4.4)	14
		Lottia strigitella species B	10.8 (4.5)	5.8 (1.7)	6
	Meiofauna abundance (# per plot)	Cirripidea	11.0 (4.4)	0.0 (0.0)	41
		Gastropods	2.8 (1.0)	2.6 (1.4)	15
		Arthropod Ostracods B	0.0 (0.0)	3.2 (1.7)	11
		Isopods	0.0 (0.0)	1.8 (0.5)	11
Middle	Cover Data	*Corallina pinnatifolia*	78.3 (6.1)	40.5 (6.3)	46
		Gelidium spp.	13.7 (13.3)	2.3 (0.8)	13
	Macroalgae presence (mean frequency)	*Centrocerus clavulatum*	0.8 (0.2)	0.2 (0.1)	13
		Chondracanthus canaliculatus	0.7 (0.2)	0.4 (0.1)	10
		Psuedolithoderma nigra	0.3 (0.2)	0.5 (0.2)	9
		Gelidium spp.	0.3 (0.2)	0.5 (0.2)	9
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	9.8 (4.5)	9.9 (5.2)	33
		Lottia scabra/conus	4.7 (2.2)	7.6 (2.1)	21
		Spirorbis spp.	3.2 (3.2)	0.0 (0.0)	9
		Nuttalina spp.	2.3 (0.7)	2.0 (0.7)	9
		Spirobranchus spp.	0.3 (0.2)	2.9 (2.0)	6
	Meiofauna abundance (# per plot)	Gastropods	75.3 (27.0)	24.3 (6.7)	58
		Sipunculids	11.5 (8.2)	3.5 (1.3)	15

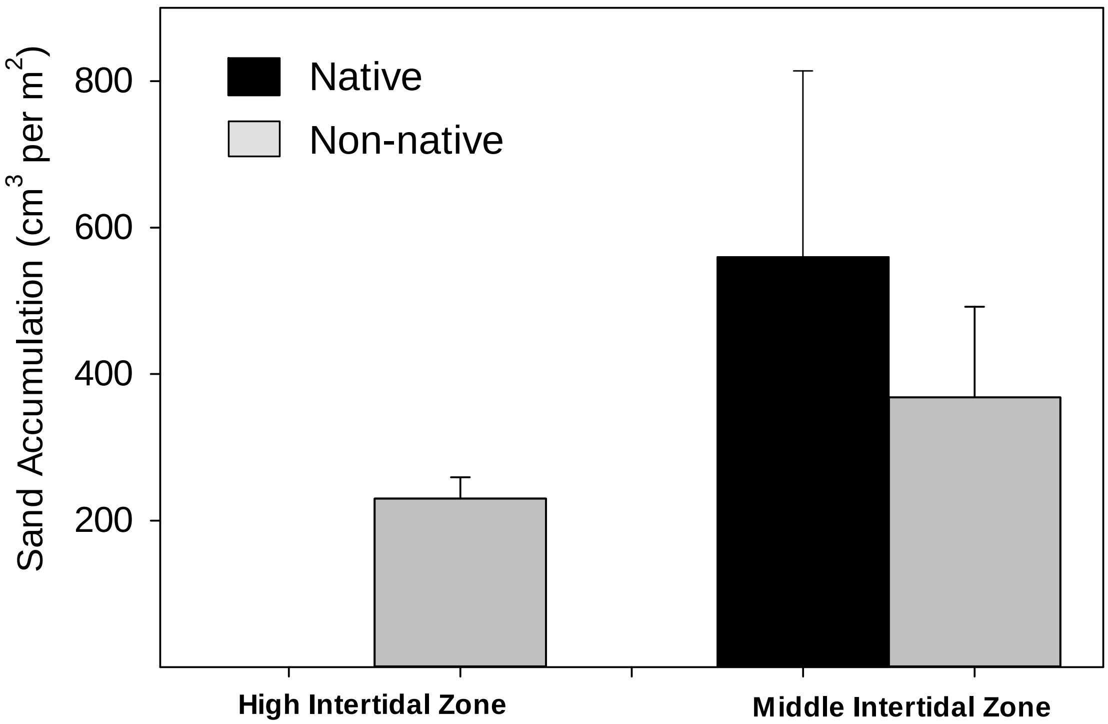

Figure 41. Sand accumulation (+/- SE) in native (black bars) and non-native (grey bars) subplots in the high and middle intertidal zone. Significant differences were observed in the high zone while no difference was observed in the middle zone (T-test).

3.22. Removal effort and success.

Scraping of small plots (400 cm^2) and burning of the rock using a torch was a relative quick process, taking ~10 minutes per plot. However, the process was destructive as all biota in plots were cleared.

The percent cover of *Caulacanthus* was significantly different among treatments prior to application of treatment (Figure 42) with the *Caulacanthus* Controls (CC; mean=59.4%) and *Caulacanthus* Removal (R; mean=61.4) being similar but having higher cover than the non-*Caulacanthus* (NC; mean=3.2) control plots (ANOVA df=2, F=66.7, p<0.001; Tukey's multiple comparisons test). There were no differences among tidal zones (ANOVA df=1, F=0.19, p=0.728). Similar patterns were observed if the tidal zones were measured separately.

The trajectory of *Caulacanthus* cover varied markedly among treatments and among zones (Figure 43). A Repeated Measures ANOVA for zones combined revealed significant differences among treatments, data, and the nested plot factor. When analyzing the zones separately, a Repeated Measures ANOVA found significant differences for both zones among treatments, data, and the nested plot factor.

	Factor	df	F stat	p-value
Zones Combined	Treatment	2	16.83	<0.001
	Zone	1	3.82	0.061
	Treatment*Zone	2	1.76	0.191
	Date	9	8.56	<0.001
	Plot (Treatment Zone)	27	4.16	<0.001
High Zone	Treatment	2	9.87	0.003
	Date	9	3.91	<0.001
	Plot (Treatment)	12	5.12	<0.001
Mid Zone	Treatment	2	6.15	0.011
	Date	9	6.36	<0.001
	Plot (Treatment)	15	3.42	<0.001

In the high zone, *Caulacanthus* control plots decreased over time, although highly variable among sampling periods (Figure 43). Removal treatments remained low for a few months but increased in cover to *Caulacanthus* Control levels mid-way through the experiment suggesting that removal had no impact. In native plots which initially had no or little *Caulacanthus*, the non-native seaweed also appeared at moderate levels in the fall season but died back again in the winter. At the end of the experiment, *Caulacanthus* was similar among the three treatment types (ANOVA df=2, F=2.15, p=0.159) despite being significantly higher in the *Caulacanthus* plots at the beginning of the experiment, prior to application of treatments (Figure 42). Overall, *Caulacanthus* in the high zone is highly variable over space and time and, observationally, appears to creep along the upper intertidal habitat, dying back and regrowing sporadically.

In the middle intertidal zone, similar patterns were observed with decreased cover in *Caulacanthus* control plots and sporadic increases in cover in non-*Caulacanthus* control plots (Figure 43). Removal treatments recovered slowly over time and matched *Caulacanthus* control plots after ~6 months. Interestingly, removal plots surpassed *Caulacanthus* control plots in later winter with the final cover in removal plots being significantly higher than *Caulacanthus* and non-*Caulacanthus* controls (Figure 42; ANOVA df=2, F=7.31, p=0.006; Tukey's multiple comparisons test). Given removal treatments cleared the plots of all biota, *Caulacanthus* may be quicker to recolonize the open space.

For all plots, it appears that the removal of *Caulacanthus* had little impact, despite the torching of the rocks to burn all living materials. Anecdotal evidence suggests that *Caulacanthus* may have survived this treatment as recovery of *Caulacanthus* within a plot often matched the spatial pattern that *Caulacanthus* was in prior to removal (see Figure 44 for an example of one plot where the growth pattern prior to removal and one year following removal are similar).

At the end of the experiment, the community composition was again assessed using abiotic and biotic cover, and macroinvertebrate counts (no subplot turf cores were conducted and seaweed presence was not analyzed). These data were analyzed similar to univariate and multivariate analyses conducted during the initial assessment with the exception of also being analyzed by treatment rather than comparing native and non-native patches. Considering the cover of *Caulacanthus* was low and highly variable at the end of the experiment, differences in assemblages are not likely reflective of the impacts of the presence or absence of *Caulacanthus*. Because of this, *Caulacanthus* cover was included in the cover analyses.

For univariate analyses comparing cover data between native and non-native patches, there were few significant differences among taxa (Table 13). In the high and middle intertidal zone, *Caulacanthus* was significantly higher in non-native plots. The articulated turf forming *Corallina pinnatifolia* and the tube forming annelid *Spirobranchus* spp. were significantly higher in native plots in the middle intertidal zone. Among treatments, the chiton *Nutallina* spp. was more common in the *Caulacanthus* Control plots in the upper intertidal zone (Table 14). In the middle intertidal zone, *Caulacanthus* was more common in the removal treatment, *Corallina pinnatifolia* more common in the non-*Caulacanthus* control plots, and the limpet *Lottia limatula* more common in the removal treatments; all other taxa were similar among treatments.

For macroinvertebrate counts, the barnacle *Chthamalus* and all barnacles together were significantly higher in native plots than non-native plots (Table 15) in the high zone. Among treatments, *Nuttalina* spp. was more common in *Caulacanthus* control plots while the limpet *Lottia strigitella* was more common in removal treatments (Table 16). In addition, *Spirobranchus* spp. was marginally higher (p=0.52) in non-*Caulacanthus* control plots.

Both species richness (Figure 45) and species diversity (H'; Figure 46) were similar in between native and non-native patches as well as among treatments in both the upper and middle intertidal zones:

	T-Test Results Native vs. Non-native						ANOVA Results by Treatment					
	Upper Zone			Middle Zone			Upper Zone			Middle Zone		
	df	T	p value	df	T	p value	df	F	pvalue	df	F	pvalue
All Cover Richness	6	1.02	0.349	10	-1.84	0.095	2	2.3	0.143	2	2.11	0.156
All Cover H'	7	-0.76	0.474	11	1.54	0.151	2	0.105	0.380	2	1.07	0.368
Macroinvertebrate Richness	5	-1.25	0.267	7	-1.83	0.110	2	2.52	0.122	2	2.12	0.154
Macroinvertebrate H'	6	-0.05	0.963	10	-2.05	0.068	2	0.47	0.635	2	2.28	0.136

Multivariate analyses of cover data reveal that assemblages were similar when comparing non-Caulacanthus plots with *Caulacanthus* plots (Figure 47 grey vs black symbols) as well as among treatments (Figure 47). Two-Factor ANOSIM revealed no difference in native vs. non-native patches but a significant difference between zones (Table 17) while ANOSIM on zones individually reveal no difference among patches for either zone. For treatments, there was a significant treatment and zone effect (Two-Factor ANOSIM) with all treatments being similar except for the removal treatment and the non-*Caulacanthus* control treatment. A significant treatment effect occurred in the middle intertidal zone with the non-*Caulacanthus* control treatment and the *Caulacanthus* removal treatment being significantly different.

For macroinvertebrate counts (Figure 48), a Two-Factor ANOSIM revealed significantly different community assemblages between patches and between zones (Table 17) but no effect when zones were analyzed separately. Equally, a Two-Factor ANOSIM revealed significantly different community assemblages between treatments and between zones (Table 17) but no effect when zones were analyzed separately. For the significant treatment effect, all treatments were similar except the removal treatment and non-*Caulacanthus* control treatment being different.

SIMPER analyses (Tables 18 and 19) show that much of the dissimilarity between patches and among treatments are driven by a small number of species such as rock, *Caulacanthus*, *Pseudolithoderma*, and *Corallina* for cover data and *Chthamalus*, *Littorina*, and various limpets species for macroinvertebrate data.

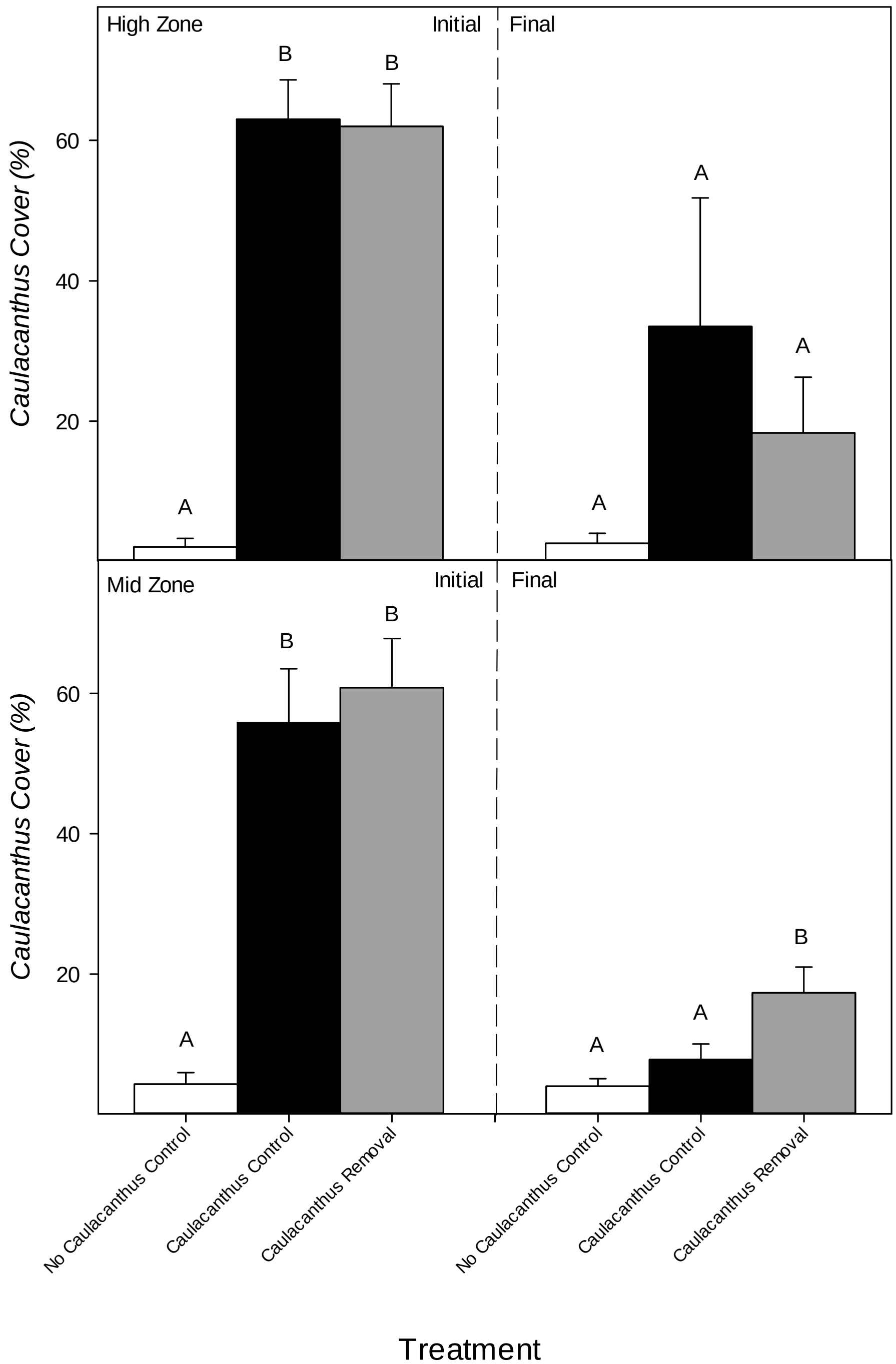

Figure 42. Mean *Caulacanthus* cover (+/- SE) for the three treatments in the high intertidal zone (upper figure) and middle intertidal zone (lower figure) prior to application of treatments and at the end of the year-long study. Letters represent significantly similar groups (ANOVA, Tukey's multiple comparisons test).

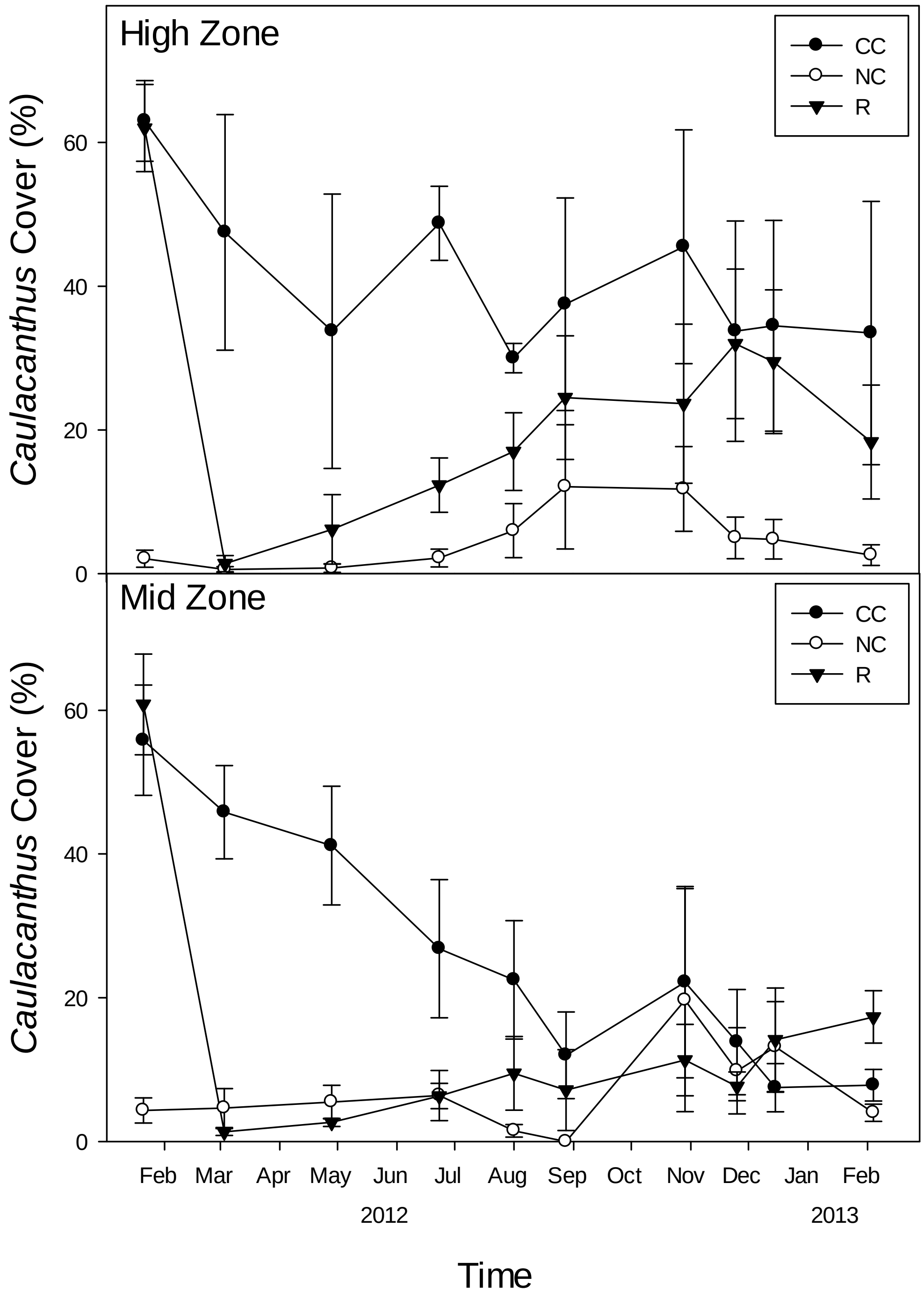

Figure 43. Mean *Caulacanthus* cover (+/- SE) in treatments over time in the high intertidal zone (upper figure) and middle intertidal zone (lower figure). (CC=Caulacanthus Control, NC=No Caulacanthus Control, R=Removal).

Figure 44. Example of a *Caulacanthus* plot showing *Caulacanthus* cover (dark red) before removal, after removal, and 1 year later. Patterns of growth before and 1 year after show similar spatial relations suggesting regrowth from crusts.

Table 13. Mean abiotic, seaweed, and macroinvertebrate cover (+/-SE) in native and non-native plots at the end of the year-long study. Designation of plots as being native or non-native were established at the beginning of the study but, by the end of the study, these designations were no longer strong descriptors as *Caulacanthus* cover varied among plots. T-Test p-values are reported for each zone separately.

	High Zone						Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value		Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Abiotic:											
Rock	76.0	4.8	41.4	10.0	0.064		10.3	3.4	21.9	5.0	0.146
Sand	0.0	0.0	1	0.5	0.162		1.8	0.8	3.9	0.9	0.160
Seaweeds:											
Caulacanthus ustulatus	2.6	1.4	24.4	8.5	**0.052**		4.0	1.1	12.6	2.5	**0.032**
Centrocera clavulatum							0.3	0.3	0.1	0.1	0.346
Ceramium spp.							0.0	0.0	0.1	0.1	0.496
Chondracanthus canaliculatus							1.3	1.0	0.3	0.2	0.176
Cladophora spp.							0.1	0.1	0.3	0.2	0.537
Colpomenia sinuosa							0.3	0.2	0.1	0.1	0.258
Corallina pinnatifolia	0.0	0.0	3.95	2.7	0.424		57.0	7.0	28.1	5.8	**0.009**
Crustose Coralline	2.0	1.2	2	0.6	1.000		7.7	2.4	3.9	1.1	0.125
Gelidium pusillum	0.0	0.0	7.2	6.0	0.453		5.3	4.0	2.9	1.6	0.510
Hildenbrandia	0.2	0.2	0	0.0	0.220						
Laurencia pacifica							0.2	0.2	0.1	0.1	0.621
Lithothrix aspergillum	0.0	0.0	0.2	0.2	0.453		8.0	5.1	8.4	4.0	0.951
Lomentaria hakodotensis							0.2	0.2	0.8	0.5	0.377
Osmundea sinicola							0.1	0.1	0.0	0.0	0.163
Petrospongium rugosom	1.0	0.8	0.5	0.3	0.630		0.0	0.0	0.9	0.4	0.161
Psuedolithoderma nigra	10.2	3.5	8.4	2.7	0.344		7.8	3.2	10.8	4.0	0.631
Pterocadiella capilacea							0.3	0.3	0.0	0.0	0.163
Ralfsia	0.0	0.0	0.5	0.5	0.453		0.0	0.0	0.1	0.1	0.496
Scytosiphon lometaria	1.0	1.0	8.6	5.8	0.308		0.0	0.0	0.2	0.2	0.496
Silvetia compressa							0.0	0.0	1.0	1.0	0.496
Ulva californica	0.0	0.0	1.15	0.5	0.115		5.7	2.0	7.6	2.3	0.601

Table 13 Continued.

	High Zone					Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Invertebrates:										
Agnathostoma eiseni						0.5	0.5	0.1	0.1	0.267
Anthopleura spp.	1.1	1.0	0.4	0.2	0.479	1.2	0.6	0.3	0.2	0.068
Balanus glandula	0.4	0.2	0.1	0.1	0.065	0.3	0.1	0.4	0.2	0.659
Bulla bulla						0.1	0.1	0.0	0.0	0.621
Chlorostoma funebralis	0.0	0.0	0.4	0.4	0.453	0.1	0.1	0.0	0.0	0.163
Chthamalus spp	6.6	4.7	0.15	0.1	0.099	0.5	0.0	0.8	0.3	0.437
Cyanoplax hartwegii	0.0	0.0	0.15	0.1	0.291					
Fisurella volcano						0.1	0.1	0.1	0.1	1.000
Littorina spp.	0.7	0.3	0.5	0.2	0.638	0.1	0.1	0.1	0.1	1.000
Lottia digitalis	0.1	0.1	0.05	0.1	0.742					
Lottia limatula	0.0	0.0	0.3	0.1	0.174	0.2	0.1	0.4	0.2	0.438
Lottia scabra/conus	0.9	0.1	0.65	0.1	0.151	0.3	0.1	1.0	0.3	0.125
Lottia strigitella	0.8	0.3	0.7	0.3	0.980	0.1	0.1	0.4	0.2	0.208
Mopalia muscosa						0.3	0.3	0.0	0.0	0.163
Mytilus californianus	0.1	0.1	0	0.0	0.220					
Navanax						0.0	0.0	0.0	0.0	0.496
Nuttalina spp	0.4	0.2	0.45	0.1	0.702	0.3	0.1	0.8	0.2	0.201
Pachygrapsus crassipes	0.0	0.0	0.05	0.1	0.453	0.1	0.1	0.0	0.0	0.621
Pagurus hirsuticulus	0.0	0.0	0.05	0.1	0.453					
Pagurus samuelis						0.0	0.0	0.0	0.0	0.496
Phragmatopoma californica						0.0	0.0	0.2	0.2	0.496
Psuedochema exogyra						0.0	0.0	0.2	0.2	0.496
Septifer bifurcatus	0.3	0.1	0.25	0.1	0.935	0.1	0.1	0.1	0.1	0.709
Serpulorbis squamigerus						0.4	0.2	0.2	0.2	0.464
Spirobranchus spp.						0.3	0.1	0.1	0.1	**0.035**
Sprirorbis spp.						0.3	0.3	0.0	0.0	0.234
Tetraclita rubescens						0.1	0.1	0.0	0.0	0.163
Total biotic	28.4	4.1	61.25	12.3	0.133	103.6	8.4	83.5	6.0	0.071

Table 14. Mean abiotic, seaweed, and macroinvertebrate cover (+/-SE) in treatments plots (Non-*Caulacanthus* Control, *Caulacanthus* Control, and *Caulacanthus* Removal) at the end of the year-long study. ANOVA p-values are reported for each zone separately.

	High Zone							Middle						
	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value
Abiotic:														
Rock	76.0	4.8	46.8	18.5	37.8	12.4	0.148	10.3	3.4	17.2	6.0	26.7	8.1	0.203
Sand	0.0	0.0	1.0	0.7	1.0	0.8	0.106	1.8	0.8	4.2	1.4	3.7	1.2	0.368
Seaweeds:														
Caulacanthus ustulatus	2.6	1.4	33.5	18.3	18.3	7.9	0.159	4.0	1.1	7.8	2.2	17.3	3.6	**0.006**
Centrocera clavulatum								0.3	0.3	0.2	0.2	0.0	0.0	0.561
Ceramium spp.								0.0	0.0	0.2	0.2	0.0	0.0	0.391
Chondracanthus canaliculatus								1.3	1.0	0.7	0.3	0.0	0.0	0.300
Cladophora spp.								0.1	0.1	0.5	0.3	0.0	0.0	0.209
Colpomenia sinuosa								0.3	0.2	0.2	0.1	0.0	0.0	0.327
Corallina pinnatifolia	0.0	0.0	6.5	6.2	2.3	2.2	0.410	57.0	7.0	35.3	6.8	20.8	9.1	**0.015**
Crustose Coralline	2.0	1.2	3.0	0.7	1.3	0.7	0.481	7.7	2.4	4.7	2.1	3.2	1.0	0.277
Gelidium pusillum	0.0	0.0	3.0	3.0	10.0	10.0	0.585	5.3	4.0	5.0	3.1	0.8	0.8	0.496
Hildenbrandia	0.2	0.2	0.0	0.0	0.0	0.0	0.397							
Laurencia pacifica								0.2	0.2	0.2	0.2	0.0	0.0	0.616
Lithothrix aspergillum	0.0	0.0	0.5	0.5	0.0	0.0	0.269	8.0	5.1	15.8	6.9	1.0	0.5	0.139
Lomentaria hakodotensis								0.2	0.2	0.8	0.8	0.8	0.7	0.686
Osmundea sinicola								0.1	0.1	0.0	0.0	0.0	0.0	0.391
Petrospongium rugosom	1.0	0.8	0.3	0.3	0.7	0.5	0.690	0.0	0.0	0.3	0.3	1.5	0.8	0.101
Psuedolithoderma nigra	10.2	3.5	5.8	2.5	10.2	4.2	0.674	7.8	3.2	5.3	1.1	16.3	7.5	0.262
Pterocadiella capilacea								0.3	0.3	0.0	0.0	0.0	0.0	0.391
Ralfsia	0.0	0.0	0.0	0.0	0.8	0.8	0.507	0.0	0.0	0.0	0.0	0.2	0.2	0.391
Scytosiphon lometaria	1.0	1.0	8.8	8.8	8.5	8.3	0.689	0.0	0.0	0.0	0.0	0.3	0.3	0.391
Silvetia compressa								0.0	0.0	2.0	2.0	0.0	0.0	0.391
Ulva californica	0.0	0.0	1.8	1.1	0.8	0.5	0.194	5.7	2.0	6.7	2.0	8.5	4.4	0.799

Table 14 Continued

	High Zone							Middle						
	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value
Invertebrates:														
Agnathostoma eiseni								0.5	0.5	0.2	0.2	0.0	0.0	0.512
Anthopleura spp.	1.1	1.0	0.9	0.4	0.1	0.1	0.443	1.2	0.6	0.5	0.3	0.0	0.0	0.133
Balanus glandula	0.4	0.2	0.0	0.0	0.2	0.1	0.162	0.3	0.1	0.3	0.2	0.4	0.3	0.882
Bulla bulla								0.1	0.1	0.0	0.0	0.1	0.1	0.616
Chlorostoma funebralis	0.0	0.0	1.0	1.0	0.0	0.0	0.269	0.1	0.1	0.0	0.0	0.0	0.0	0.391
Chthamalus spp	6.6	4.7	0.1	0.1	0.2	0.1	0.191	0.5	0.0	0.8	0.5	0.9	0.4	0.705
Cyanoplax hartwegii	0.0	0.0	0.0	0.0	0.3	0.2	0.253							
Fisurella volcano								0.1	0.1	0.1	0.1	0.1	0.1	1.000
Littorina spp.	0.7	0.3	0.4	0.2	0.6	0.3	0.798	0.1	0.1	0.2	0.1	0.0	0.0	0.342
Lottia digitalis	0.1	0.1	0.1	0.1	0.0	0.0	0.511							
Lottia limatula	0.0	0.0	0.4	0.2	0.3	0.2	0.309	0.2	0.1	0.2	0.1	0.6	0.3	0.290
Lottia scabra/conus	0.9	0.1	0.5	0.0	0.8	0.2	0.178	0.3	0.1	0.5	0.1	1.5	0.5	**0.028**
Lottia strigitella	0.8	0.3	0.4	0.1	0.9	0.4	0.596	0.1	0.1	0.2	0.1	0.7	0.3	0.103
Mopalia muscosa								0.3	0.3	0.0	0.0	0.0	0.0	0.391
Mytilus californianus	0.1	0.1	0.0	0.0	0.0	0.0	0.397							
Navanax								0.0	0.0	0.0	0.0	0.1	0.1	0.391
Nuttalina spp	0.4	0.2	0.9	0.1	0.2	0.1	**0.016**	0.3	0.1	0.9	0.4	0.7	0.3	0.376
Pachygrapsus crassipes	0.0	0.0	0.0	0.0	0.1	0.1	0.507	0.1	0.1	0.1	0.1	0.0	0.0	0.616
Pagurus hirsuticulus	0.0	0.0	0.0	0.0	0.1	0.1	0.507							
Pagurus samuelis	0.0	0.0	0.0	0.0	0.1	0.1	0.507	0.0	0.0	0.1	0.1	0.0	0.0	0.391
Phragmatopoma californica	0.0	0.0	0.0	0.0	0.2	0.2	0.507	0.0	0.0	0.0	0.0	0.3	0.3	0.391
Psuedochema exogyra								0.0	0.0	0.0	0.0	0.3	0.3	0.391
Septifer bifurcatus	0.3	0.1	0.4	0.1	0.2	0.1	0.463	0.1	0.1	0.1	0.1	0.2	0.1	0.761
Serpulorbis squamigerus								0.4	0.2	0.3	0.3	0.1	0.1	0.577
Spirobranchus spp.								0.3	0.1	0.2	0.1	0.0	0.0	0.048
Sprirorbis spp.								0.3	0.3	0.1	0.1	0.0	0.0	0.483
Tetraclita rubescens								0.1	0.1	0.0	0.0	0.0	0.0	0.391
Total biotic	28.4	4.1	68.0	25.0	56.8	13.9	0.224	103.6	8.4	90.3	8.2	76.8	8.7	0.112

Table 15. Mean macroinvertebrate counts (+/-SE) in native and non-native plots at the end of the year-long study. Designation of plots as being native or non-native were established at the beginning of the study but, by the end of the study, these designations were no longer strong descriptors as *Caulacanthus* cover varied among plots. T-Test p-values are reported for each zone separately.

	High Zone					Middle				
	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value	Native Mean	Native SE	Non-Native Mean	Non-Native SE	T-test p-value
Agnathostoma eiseni						0.7	0.7	0.3	0.3	0.483
Anthopleura spp.	3.0	2.3	0.9	0.5	0.248	1.5	0.6	0.5	0.3	0.081
Balanus glandula	6.2	4.8	0.2	0.1	0.087	1.2	0.6	2.0	1.0	0.597
Bulla bulla						1.0	1.0	0.1	0.1	0.206
Chlorostoma funebralis	0.0	0.0	1.4	1.4	0.500	0.2	0.2	0.0	0.0	0.163
Chthamalus spp	99.6	63.4	1.5	1.0	**0.040**	6.8	1.9	14.0	4.7	0.308
Cyanoplax hartwegii	0.0	0.0	0.3	0.2	0.347					
Fisurella volcano						0.2	0.2	0.2	0.1	1.000
Littorina spp.	16.8	10.0	9.0	4.8	0.435	0.3	0.3	0.2	0.1	0.559
Lottia digitalis	0.2	0.2	0.1	0.1	0.622					
Lottia limatula	0.0	0.0	0.9	0.4	0.173	0.7	0.5	0.6	0.3	0.871
Lottia scabra/conus	16.8	6.4	10.1	2.8	0.274	6.5	3.1	8.8	1.6	0.462
Lottia strigitella	7.0	4.3	5.4	2.1	0.710	0.2	0.2	1.7	0.7	0.175
Mopalia muscosa						0.2	0.2	0.0	0.0	0.163
Mytilus californianus	0.4	0.4	0.0	0.0	0.165					
Navanax						0.0	0.0	0.1	0.1	0.496
Nuttalina spp	0.6	0.2	0.9	0.3	0.500	2.3	0.9	1.6	0.4	0.391
Pachygrapsus crassipes	0.0	0.0	0.1	0.1	0.500	0.3	0.2	0.1	0.1	0.201
Pagurus hirsuticulis	0.0	0.0	0.1	0.1	0.500	0.0	0.0	0.1	0.1	0.496
Pagurus samuelis	0.0	0.0	0.9	0.9	0.500	0.0	0.0	0.3	0.3	0.496
Phragmatopoma californica	0.0	0.0	0.2	0.2	0.500	0.0	0.0	0.2	0.2	0.496
Psuedochema exogyra						0.0	0.0	0.1	0.1	0.496
Septifer bifurcatus	3.8	2.1	2.2	1.0	0.439	1.5	1.5	0.5	0.3	0.380
Serpulorbis squamigerus						1.7	0.9	0.2	0.1	**0.035**
Spirobranchus spp.						1.8	0.8	0.3	0.2	0.018
Sprirorbis spp.						10.0	10.0	0.8	0.8	0.206
Tetraclita rubescens						0.2	0.2	0.0	0.0	0.163
All Limpets	24.0	8.1	16.5	3.7	0.344	7.3	3.3	11.1	1.9	0.311
All Barnacles	105.8	68.1	1.7	1.1	**0.043**	8.2	2.3	16.0	5.0	0.306

Table 16. Mean macroinvertebrate count (+/-SE) in treatments plots (Non-*Caulacanthus* Control, *Caulacanthus* Control, and *Caulacanthus* Removal) at the end of the year-long study. ANOVA p-values are reported for each zone separately.

	High Zone							Middle						
	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value	Non-*Caulacanthus* Control Mean	Non-*Caulacanthus* Control SE	*Caulacanthus* Control Mean	*Caulacanthus* Control SE	*Caulacanthus* Removal Mean	*Caulacanthus* Removal SE	ANOVA p value
Agnathostoma eiseni	0.0	0.0	0.0	0.0	0.0	0.0		0.7	0.7	0.5	0.5	0.0	0.0	0.605
Anthopleura spp.	3.0	2.3	2.0	1.1	0.2	0.2	0.361	1.5	0.6	1.0	0.4	0.0	0.0	0.061
Balanus glandula	6.2	4.8	0.0	0.0	0.3	0.2	0.244	1.2	0.6	2.5	1.7	1.5	1.3	0.753
Bulla bulla	0.0	0.0	0.0	0.0	0.0	0.0		1.0	1.0	0.0	0.0	0.2	0.2	0.452
Chlorostoma funebralis	0.0	0.0	3.5	3.5	0.0	0.0	0.269	0.2	0.2	0.0	0.0	0.0	0.0	0.391
Chthamalus spp	99.6	63.4	1.0	1.0	1.8	1.6	0.134	6.8	1.9	9.7	5.7	18.3	7.5	0.335
Cyanoplax hartwegii	0.0	0.0	0.0	0.0	0.5	0.3	0.253	0.0	0.0	0.0	0.0	0.0	0.0	
Fisurella volcano	0.0	0.0	0.0	0.0	0.0	0.0		0.2	0.2	0.2	0.2	0.2	0.2	1.000
Littorina spp.	16.8	10.0	12.0	10.1	7.0	5.1	0.683	0.3	0.3	0.3	0.2	0.0	0.0	0.505
Lottia digitalis	0.2	0.2	0.3	0.3	0.0	0.0	0.511	0.0	0.0	0.0	0.0	0.0	0.0	
Lottia limatula	0.0	0.0	1.5	1.0	0.5	0.3	0.164	0.7	0.5	0.3	0.2	0.8	0.5	0.693
Lottia scabra/conus	16.8	6.4	12.0	5.8	8.8	2.9	0.511	6.5	3.1	9.0	2.6	8.7	2.0	0.767
Lottia strigitella	7.0	4.3	2.8	1.4	7.2	3.3	0.643	0.2	0.2	0.3	0.2	3.0	1.3	**0.029**
Mopalia muscosa	0.0	0.0	0.0	0.0	0.0	0.0		0.2	0.2	0.0	0.0	0.0	0.0	0.391
Mytilus californianus	0.4	0.4	0.0	0.0	0.0	0.0	0.397	0.0	0.0	0.0	0.0	0.0	0.0	
Navanax	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.2	0.2	0.391
Nuttalina spp	0.6	0.2	1.8	0.3	0.3	0.2	**0.004**	2.3	0.9	1.8	0.7	1.3	0.5	0.619
Pachygrapsus crassipes	0.0	0.0	0.0	0.0	0.2	0.2	0.507	0.3	0.2	0.2	0.2	0.0	0.0	0.342
Pagurus hirsuticulis	0.0	0.0	0.0	0.0	0.2	0.2	0.507	0.0	0.0	0.0	0.0	0.2	0.2	0.391
Pagurus samuelis	0.0	0.0	0.0	0.0	1.5	1.5	0.507	0.0	0.0	0.7	0.7	0.0	0.0	0.391
Phragmatopoma californica	0.0	0.0	0.0	0.0	0.3	0.3	0.507	0.0	0.0	0.0	0.0	0.3	0.3	0.391
Psuedochema exogyra	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.2	0.2	0.391
Septifer bifurcatus	3.8	2.1	4.8	1.8	0.5	0.3	0.135	1.5	1.5	0.5	0.5	0.5	0.3	0.689
Serpulorbis squamigerus	0.0	0.0	0.0	0.0	0.0	0.0		1.7	0.9	0.2	0.2	0.2	0.2	0.116
Spirobranchus spp.	0.0	0.0	0.0	0.0	0.0	0.0		1.8	0.8	0.5	0.3	0.0	0.0	**0.052**
Sprirorbis spp.	0.0	0.0	0.0	0.0	0.0	0.0		10.0	10.0	1.7	1.7	0.0	0.0	0.452
Tetraclita rubescens	0.0	0.0	0.0	0.0	0.0	0.0		0.2	0.2	0.0	0.0	0.0	0.0	0.391
All Limpets	24.0	8.1	16.5	6.4	16.5	5.0	0.650	7.3	3.3	9.7	2.7	12.5	2.9	0.487
All Barnacles	105.8	68.1	1.0	1.0	2.2	1.8	0.139	8.2	2.3	12.2	6.6	19.8	7.9	0.409

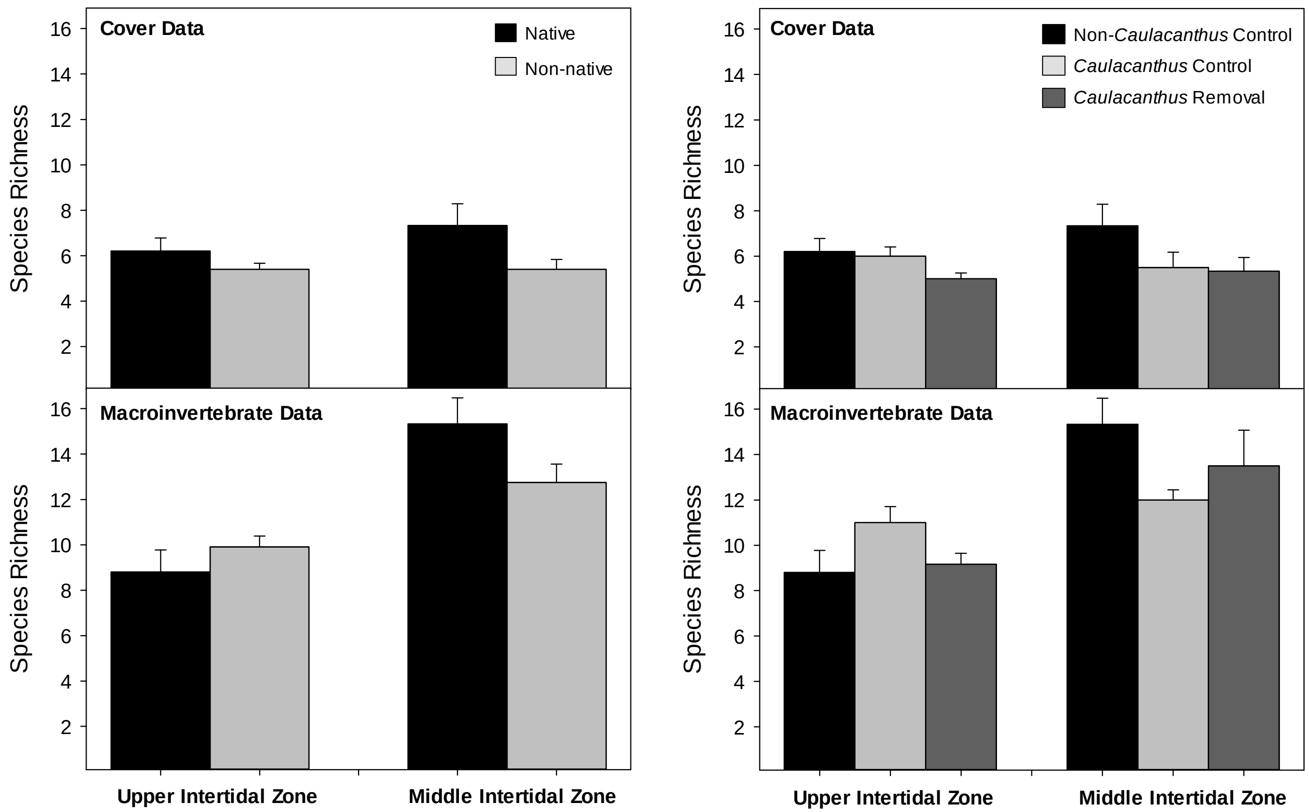

Figure 45. Mean species richness (+/- SE) for cover data (upper figures) and macroinvertebrate data (lower figures) in both the upper and middle intertidal zones, comparing between native and non-native patches (left figures) and among treatments (right figures).

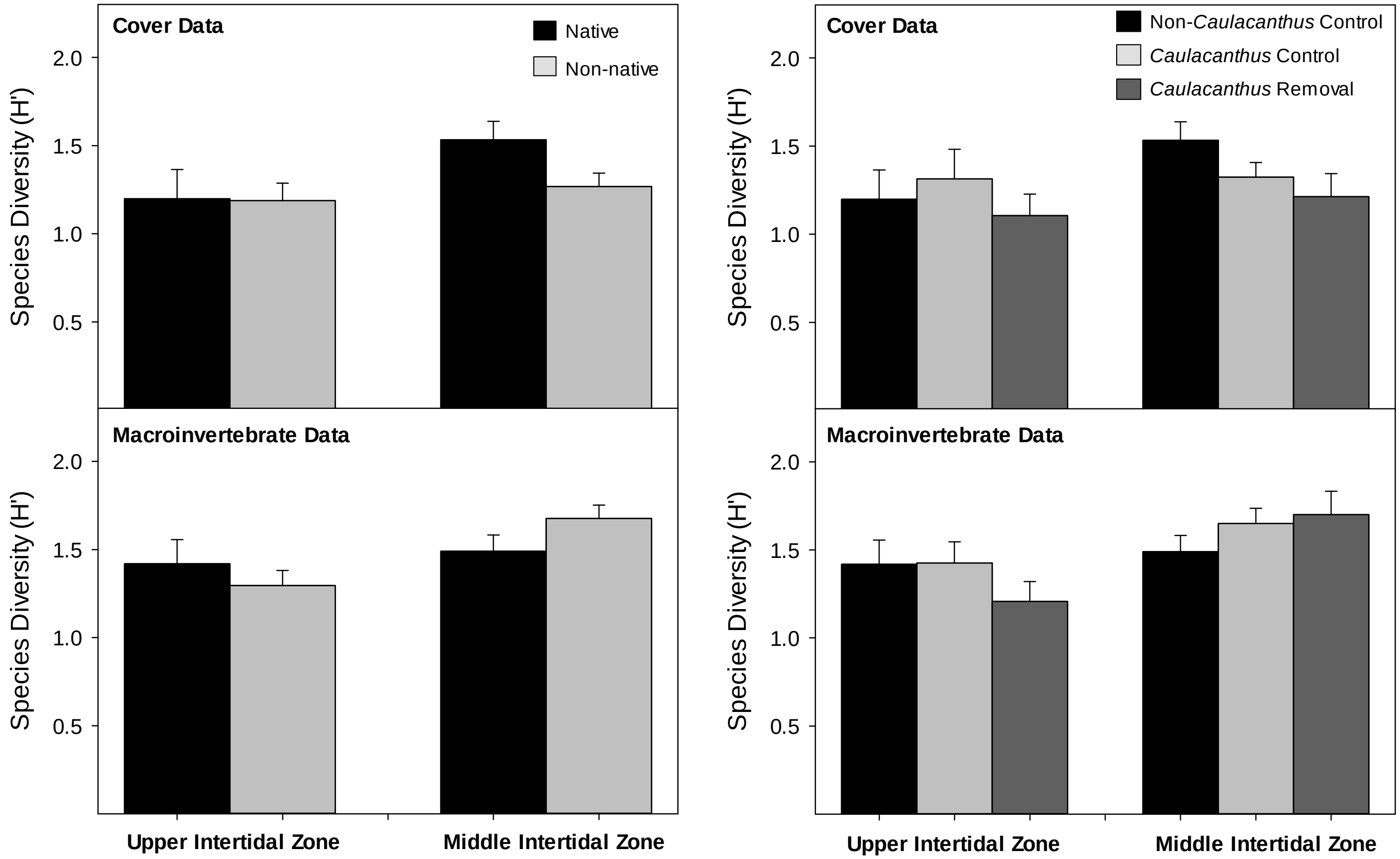

Figure 46. Mean species diversity (H'; +/- SE) for cover data (upper figures) and macroinvertebrate data (lower figures) in both the upper and middle intertidal zones, comparing between native and non-native patches (left figures) and among treatments (right figures).

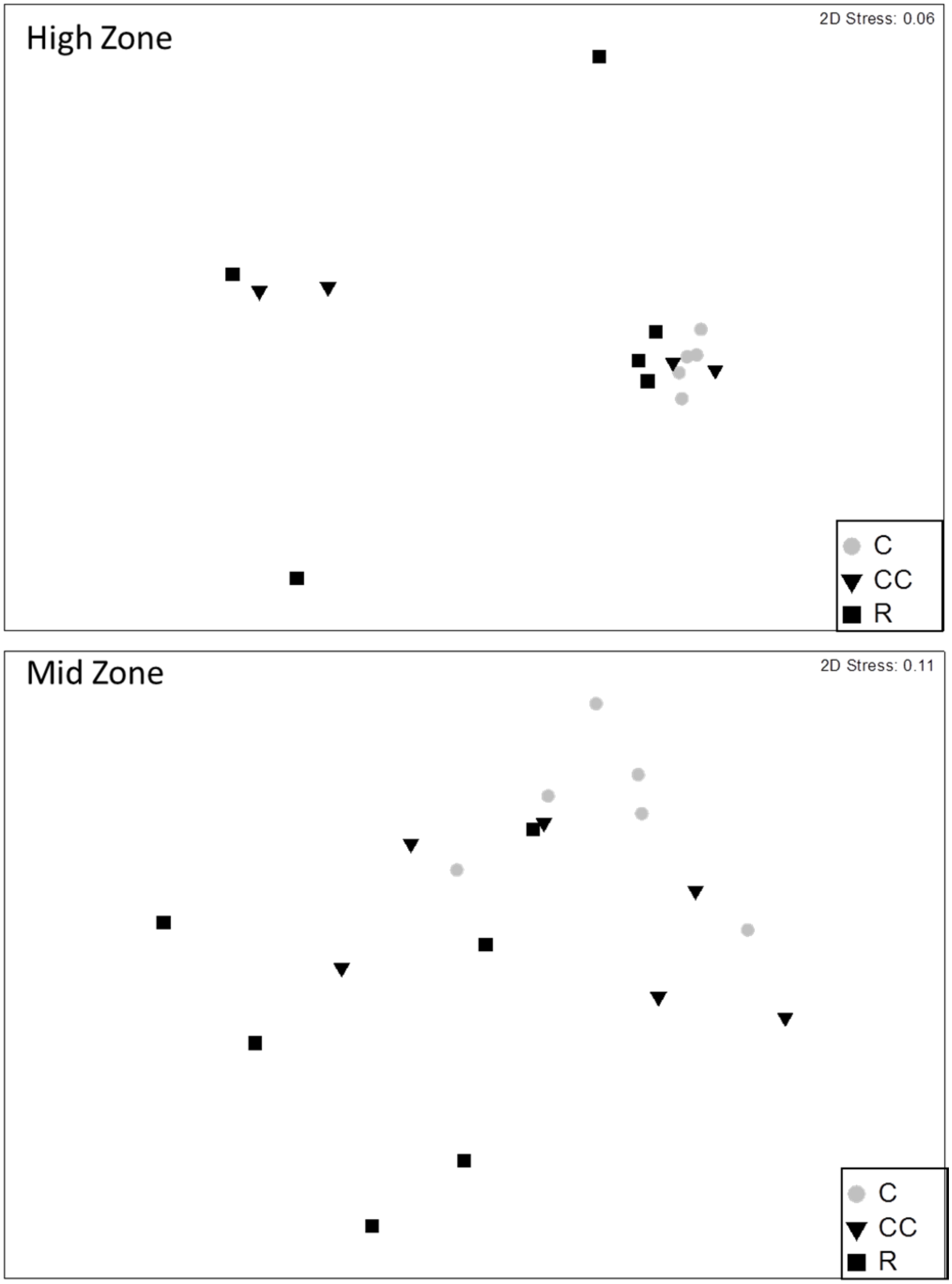

Figure 47. Multidimensional scaling plot for community assemblages using cover data in native (grey circles) and non-native patches (black symbols) and among treatments (C=Non-*Caulacanthus* control, CC=*Caulacanthus* control, R=*Caulacanthus* removal) in the upper and middle intertidal zones.

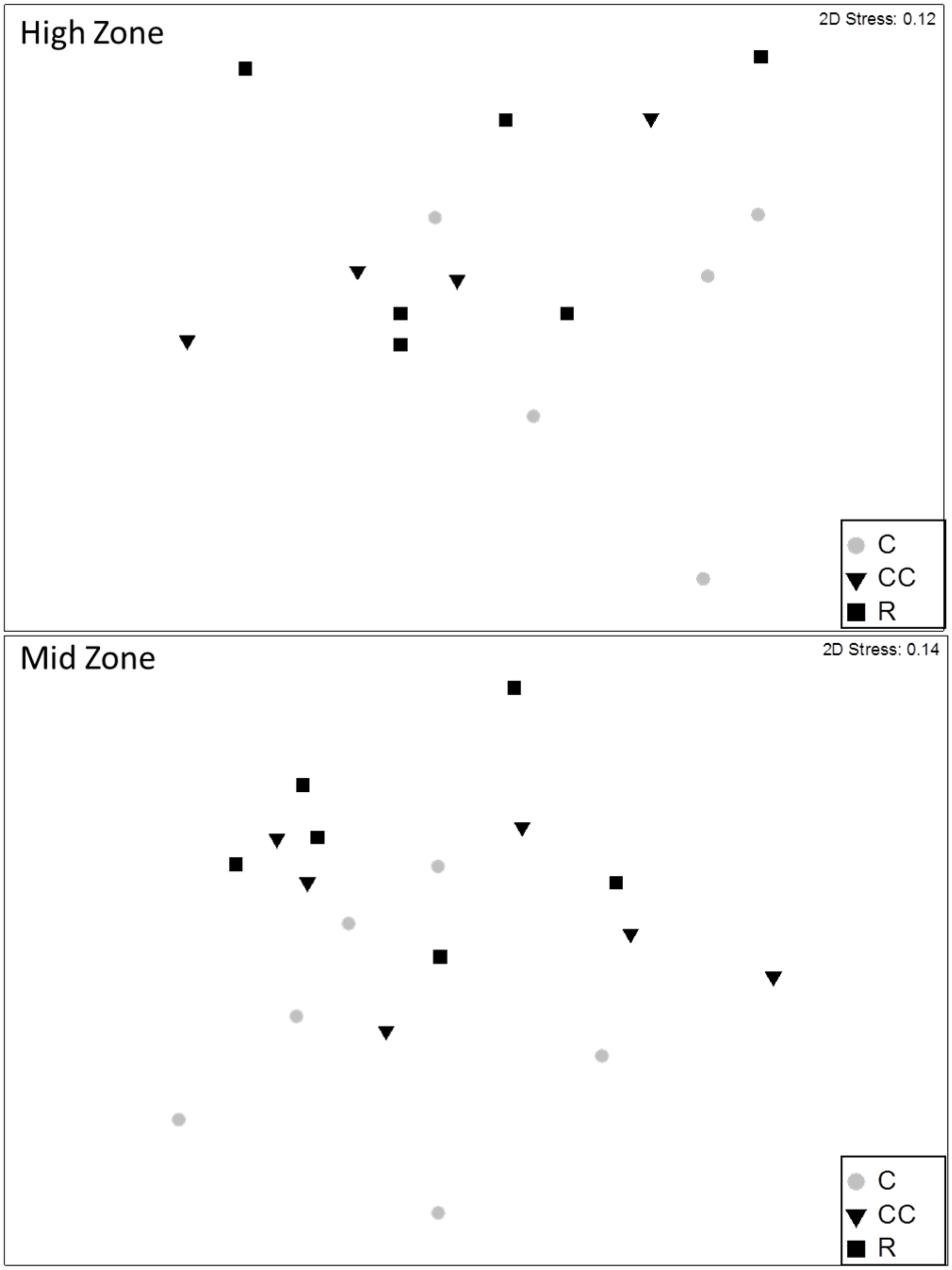

Figure 48. Multidimensional scaling plot for community assemblages using cover data in native (grey circles) and non-native patches (black symbols) and among treatments (C=Non-*Caulacanthus* control, CC=*Caulacanthus* control, R=*Caulacanthus* removal) in the upper and middle intertidal zones.

Table 17. ANOSIM results comparing community structure using both cover data and macroinvertebrate abundances. Two-Factor ANOSIM compare zones and either patches (native vs non-native) or treatments. Also included are ANOSIM results for the upper and middle intertidal zone separately for patches and treatments.

	Two-Factor ANOSIM Results				ANOSIM Results			
	Patch		Zone		Patch: Upper Zone		Patch: Middle Zone	
	Global R	p value	Global R	p value	Global R	p value	Global R	p value
All cover data (%, abiotic and Caulacanthus included)	0.016	0.350	0.416	**0.001**	-0.036	0.527	0.05	0.276
Macroinvertebrate abundance (# per plot)	0.160	**0.034**	0.201	**0.005**	0.174	0.099	0.151	0.103
	Two-Factor ANOSIM Results				ANOSIM Results			
	Treatment		Zone		Treatment: Upper Zone		Treatment: Middle Zone	
	Global R	p value	Global R	p value	Global R	p value	Global R	p value
All cover data (%, abiotic and Caulacanthus included)	0.141	**0.026**	0.494	**0.001**	0.047	0.247	0.206	**0.017**
Macroinvertebrate abundance (# per plot)	0.083	**0.010**	0.206	**0.010**	0.132	0.099	0.049	0.236
In cases with Treatment significance, C≠R; R=CC; C=CC								

Table 18. SIMPER results for species contributing most to dissimilarity between native and non-native patches in the upper and middle intertidal zones for both cover and macroinvertebrate count data sets.

Intertidal Zone	**Data Set**	**Species**	**Native**	**Non-native**	**~ Dissimilarity Contribution (%)**
Upper	Cover Data	Rock	76 (4.8)	41.4 (10)	36
		Caulacanthus ustulatus	2.6 (1.4)	24.4 (8.5)	20
		Psuedolithoderma nigra	10.2 (3.5)	8.4 (2.7)	8
		Scytosiphon lomentaria	1.0 (1.0)	8.6 (5.8)	8
		Gelidium spp.	0.0 (0.0)	7.2 (6.0)	7
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	99.6 (63.4)	1.5 (1.0)	49
		Littorina spp	16.8 (10.0)	9.0 (4.8)	18
		Lottia scabra/conus	16.8 (6.4)	10.1 (2.8)	9
		Lottia strigitella	7.0 (4.3)	5.4 (2.1)	8
Middle	Cover Data	*Corallina pinnatifolia*	57.0 (7.0)	28.1 (5.8)	28
		Rock	10.3 (3.4)	21.9 (5.0)	14
		Lithothrix aspergillum	8.0 (5.1)	8.4 (4.0)	10
		Psuedolithoderma nigra	7.8 (3.2)	10.8 (4.0)	9
		Caulacanthus ustulatus	4.0 (1.1)	12.6 (2.5)	9
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	6.8 (1.9)	14.0 (4.7)	28
		Lottia scabra/conus	6.5 (3.1)	8.8 (1.6)	17
		Spirorbis spp.	10.0 (10.0)	0.8 (0.8)	13

Table 19 SIMPER results for species contributing most to dissimilarity between pairwise comparisons of the three treatments in the upper and middle intertidal zones for both cover and macroinvertebrate count data sets.

Intertidal Zone	**Data Set**	**Species**	**Non-*Caulacanthus* Control**	***Caulacanthus* Removal**	**~ Dissimilarity Contribution (%)**
Upper	Cover Data	Rock	76 (4.8)	37.8 (12.4)	40
		Caulacanthus ustulatus	2.6 (1.4)	18.3 (7.9)	15
		Psuedolithoderma nigra	10.2 (3.5)	10.2 (4.2)	9
		Gelidium spp.	0.0 (0.0)	10.0 (10.0)	9
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	99.6 (63.4)	1.8 (1.6)	49
		Littorina spp	16.8 (10.0)	7.0 (5.1)	18
		Lottia strigitella	7.0 (4.3)	7.2 (3.3)	9
		Lottia scabra/conus	16.8 (6.4)	8.8 (2.9)	9
Middle	Cover Data	*Corallina pinnatifolia*	57.0 (7.0)	20.8 (9.1)	30
		Rock	10.3 (3.4)	26.7 (8.1)	15
		Psuedolithoderma nigra	7.8 (3.2)	16.3 (7.5)	11
		Caulacanthus ustulatus	4.0 (1.1)	17.3 (3.6)	11
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	6.8 (1.9)	18.3 (7.5)	32
		Lottia scabra/conus	6.5 (3.1)	8.7 (2.0)	15
		Spirorbis spp.	10.0 (10.0)	0.0 (0.0)	11

Intertidal Zone	**Data Set**	**Species**	**Non-*Caulacanthus* Control**	***Caulacanthus* Control**	**~ Dissimilarity Contribution (%)**
Upper	Cover Data	Rock	76 (4.8)	46.8 (18.5)	30
		Caulacanthus ustulatus	2.6 (1.4)	33.5 (18.3)	28
		Scytosiphon lomentaria	1.0 (1.0)	8.8 (8.5)	8
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	99.6 (63.4)	1.0 (0.8)	48
		Littorina spp	16.8 (10.0)	12.0 (8.2)	19
		Lottia scabra/conus	16.8 (6.4)	12.0 (4.8)	10
Middle	Cover Data	*Corallina pinnatifolia*	57.0 (7.0)	35.3 (6.8)	26
		Lithothrix aspergillum	8.0 (5.1)	15.8 (6.9)	16
		Rock	10.3 (3.4)	17.2 (6.0)	13
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	6.8 (1.9)	9.7 (5.7)	25
		Lottia scabra/conus	6.5 (3.1)	9.0 (2.6)	19
		Spirorbis spp.	10.0 (10.0)	1.7 (1.7)	15

Intertidal Zone	**Data Set**	**Species**	***Caulacanthus* Control**	***Caulacanthus* Removal**	**~ Dissimilarity Contribution (%)**
Upper	Cover Data	Rock	46.8 (18.5)	37.8 (12.4)	30
		Caulacanthus ustulatus	33.5 (18.3)	18.3 (7.9)	25
		Scytosiphon lomentaria	8.8 (8.5)	8.5 (8.8)	11
		Gelidium spp.	3.0 (3.0)	10.0 (10.0)	10
	Macroinvertebrate abundance (# per plot)	*Littorina* spp	12.0 (8.2)	7.0 (5.1)	27
		Lottia scabra/conus	12.0 (4.8)	8.8 (2.9)	19
		Lottia strigitella	2.8 (1.4)	7.2 (3.3)	12
		Septifer bifurcatus	4.8 (1.8)	0.5 (0.3)	11
		Chlorostoma funebralis	3.5 (3.5)	0.0 (0.0)	9
Middle	Cover Data	*Corallina pinnatifolia*	35.3 (6.8)	20.8 (9.1)	21
		Rock	17.2 (6.0)	26.7 (8.1)	16
		Lithothrix aspergillum	15.8 (6.9)	1.0 (0.5)	13
		Psuedolithoderma nigra	5.3 (1.1)	16.3 (7.5)	11
		Caulacanthus ustulatus	7.8 (2.2)	17.3 (3.6)	9
	Macroinvertebrate abundance (# per plot)	*Chthamalus* spp	9.7 (5.7)	18.3 (7.5)	40
		Lottia scabra/conus	9.0 (2.6)	8.7 (2.0)	16

3.23. Impacts of herbivorous limpets.

Caulacanthus ustulatus cover within the three plot types differed significantly over time and by plot type, indicating that the different plot types experienced different trajectories through time with plot type having a strong effect (Figure 49). In addition, the abundance of *L. scabra* within the different plots was significantly different; this was driven by the presence of limpets within removal + limpet transplant plots throughout the majority of the experiment, while being almost completely absent from the control and removal only plots:

Factor	df	F	p-value	
Limpet count	1	10.57	0.001	
Treatment	2	28.37	<0.001	*
Time	9	6.47	<0.001	
Plot (Treatment)	18	1.76	0.033	
*Not an exact F-test				

The control plots decreased in percentage cover of *Caulacanthus* over time, whereas the two removal plots (with and without limpet transplants) remained with low percentage cover throughout the experiment (Figure 49). These results were expected based on the fact that plots manipulated differently should respond differently through time. *Caulacanthus* cover was not different at the beginning of the experiment, prior to application of treatments (Figure 50; ANOVA df=2, F=0.547, p=0.588). At the end of the experiment, cover was low across all treatments (Figure 50) and significantly similar (ANOVA; df=2, F=2.23, p=0.137), which indicates that neither removal nor removal + addition of limpets had a detectable effect on *Caulacanthus* cover.

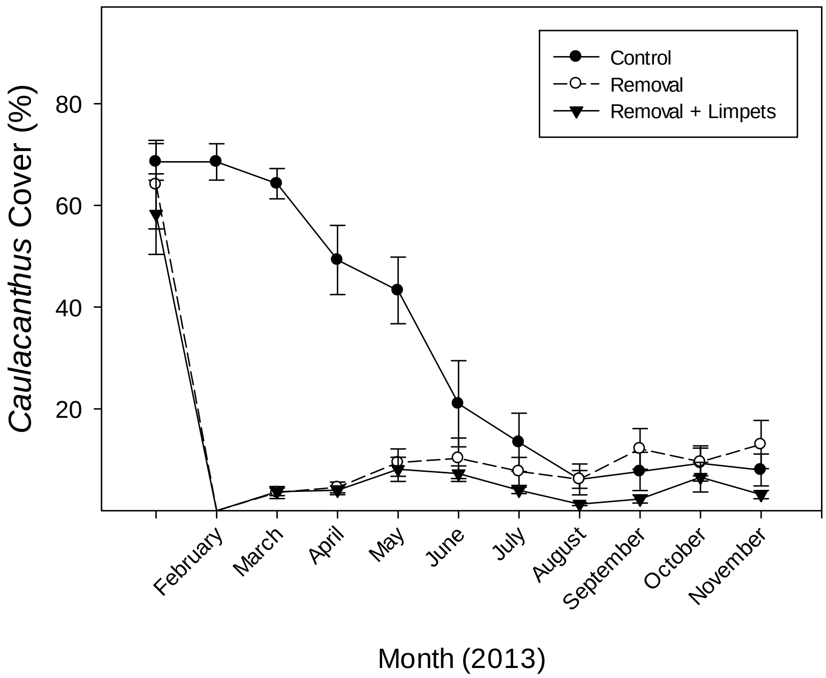

Figure 49. *Caulacanthus* cover (%; +/- SE) over time for Control plots, Removal plots, and Removal + Limpet Transplant plots.

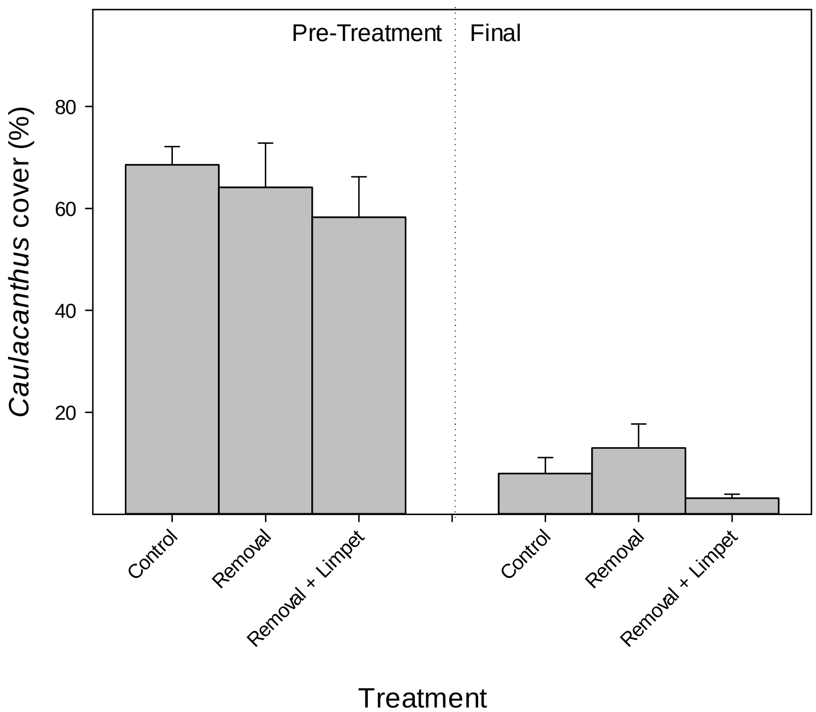

Figure 50. *Caulacanthus* cover (%; +/- SE) prior to application of treatments and at the end of the 10-month study in Control plots, Removal plots, and Removal + Limpet Transplant plots.

DISCUSSION

In the rocky intertidal ecosystem at Little Corona del Mar in Newport Beach, California, USA and in other rocky intertidal locations in southern California, the non-native seaweeds *Sargassum muticum* and *Caulacanthus ustulatus* are major contributors to community structure and ecosystem primary productivity. Examinations of the impacts of these non-native seaweeds on native assemblages are mixed. *Sargassum* had little impact on intertidal tidepools in Newport Beach despite causing marked changes in light penetration and buffering temperature changes during low tide; similar patterns were observed in this species in comparable studies worldwide while contradicting other studies that reported negative impacts. *Caulacanthus* appeared to have a negative impact on macroinvertebrates and a positive impact on seaweeds and meiofauna in the upper intertidal zone; conversely, minimal impact of *Caulacanthus* was observed in the middle intertidal zone. Zonal differences are likely due to the novel turf that *Caulacanthus* provides in the upper intertidal zone, where native seaweeds are uncommon in the region. The novel turf affords a microhabitat where sand accumulates and moisture is retained that provides refuge for seaweeds and meiofauna that normally would not be found in that habitat. In the middle intertidal zone, a native turf already exists, thus the presence of *Caulacanthus,* which often grows intertwined in the native turf, does not alter normal community structure. This study highlights that impacts can be different depending on the native taxa of concern and can vary among non-native seaweeds and within the same non-native species over different geographic regions or among different microhabitats within a location.

The ecological impact of non-native species of seaweeds has been greatly understudied. Recently, there has been an increase in research on the ecological impacts of exotic seaweeds, particularly in regards to their impacts on native species abundances, diversity, and community composition (e.g. Ceccherelli and Cinelli 1997; Williams and Grosholz 2002; Schmidt and Scheibling 2006; Thomsen et al. 2009; Byers et al. 2012; Janiak and Whitlatch 2012). The effects of non-native seaweeds on native community assemblages has been mixed, but with a majority of studies exhibiting negative impacts. For example, the non-native green alga *Caulerpa taxifolia* in the Mediterranean Sea has caused declines in algal cover (Balata et al. 2004), epifauna richness (Bellan-Santini et al. 1996), seaweed biomass (Boudouresque et al. 1992), and seagress density (Ceccherelli and Cinelli 1997) while *Fucus evanescens* in the NE Atlantic has resulted in decreases in epiflora biomass (Schueller and Peters 1994) and epiphyte biomass and richness (Wikstrom and Kautsky 2004). Alternatively, *Undaria pinnatifida* in the New Zealand region had no detectable impact on native seaweed cover or epiflora composition (Wear and Gardner 1999; Valentine and Johnson 2005) while the presence of *Gracilaria vermiculophylla* increased epifaunal abundance (Thomsen 2010; Byers et al. 2012) and filamentous algae richness and biomass (Thomsen et al 2006) in various locations globally. Despite these patterns, it must be noted that most of the published studies have been conducted on largely successful and problematic invaders while other less common non-invasive exotic species that likely have less of an impact are often ignored.

Complicating the understanding of the effects of non-native seaweeds is that the impacts can vary across spatial scales. In some locations there may be a negative impact while the same effects may not be observed in other locations. *Sargassum muticum* impacts appears to vary greatly among regions; for example, kelp and other seaweed abundances (Ambrose and Nelson 1982; DeWreede 1983, Britton-Simmons 2004) are detrimentally impacted by *Sargassum* in the NE Pacific, but other studies suggest no impact or a positive change on seaweeds on other continents (e.g. Forrest and Taylor 2002; Wernberg et al. 2004; Olabarria et al. 2009). Even within a region, the effects of *Sargassum* can vary depending on habitat. In the NE Pacific, negative effects were observed in the subtidal zone by Ambrose and Nelson (1982) and Britton Simmons (2004) yet no effects were observed in intertidal pools, as observed in this study and by Wilson (2001). The *Caulacanthus* work further suggests that impacts also can vary within different zones of an intertidal habitat as there were significant effects in the higher intertidal zone but not in the middle zone.

Equally, non-native seaweeds can have contrasting effects on different sets of taxa within a particular location, such as observed in the *Caulacanthus* study. In the upper intertidal zone, *Caulacanthus* negatively affected macroinvertebrates, but facilitated an increase in the abundance and diversity of seaweeds and meiofauna. Sánchez et al. (2005) also showed contrasting results; the presence of *Sargassum muticum* caused a decrease in seaweed biomass, but only with the fleshy seaweed functional group, while overall seaweed diversity did not change. Here, epiphytic opportunistic algae benefited from *Sargassum* due to its pattern of having a diverse epiphytic assemblage (Sánchez et al. 2005). In addition, Argyrou et al. (1999)

found that the replacement of native seagrass in Cyprus by the non-native *Caulerpa racemosa* resulted in concurrent increases in polychaetes, bivalves, and echinoderms while gastropods and crustaceans decreased in abundance. These results highlight that the impacts of non-native seaweeds should be examined across multiple types of taxa as effects can be complex.

Despite taxa-specific responses or variations among localities or habitats, a majority of non-native seaweeds are altering native communities and remain a threat to normal community assemblage composition. In addition, non-native seaweeds may have multiple indirect effects on normal ecological functioning through alteration in abundances of functional group or feeding guilds, or modifications of environmental conditions. While many of the studies speculate on possible reasons for community changes, the driving forces for community assemblage changes by non-native seaweeds represents a knowledge gap. In our study, the impacts of *Caulacanthus* in the upper intertidal zone appear to be driven by the novel creation of a turf, which rarely exists in that particular zone in this region. Conversely, despite the modification of light penetration and temperature changes in tidepools during low tides in *Sargassum* experiments in this study, no impacts were detected on native community structure. Habitat alteration also has been suggested as a driving force in other studies (e.g. Bellan-Santini et al. 1996; Relini et al. 2000; York et al. 2006; Vasquez-Luis et al. 2009). In other scenarios, changes in taxa or community composition may be driven by competition between native organisms and non-native seaweeds (Williams and Grosholz 2002; Levin et al. 2002; Scheibling and Gagon 2006; White and Shurin 2011), alterations of abiotic conditions (Tippets 2002; Strong et al. 2006), or indirect effects on epiphytic communities (Wikstrom and Kautsky 2004; Sanchez et al. 2005).

Eradication of *Sargassum* and *Caulacanthus* in this study required a high effort and was destructive to native flora and fauna. Local eradication efforts proved unsuccessful as the non-native seaweeds recovered to levels equal to that of non-manipulated plots. The manipulations of herbivores, in concert with removal, also proved unsuccessful for both non-native seaweeds. The combination of minimal impacts on native species, the high effort required for removal, and quick recovery suggest that efforts to eradicate these species are not worthy of consideration.

Eradication and control efforts have been conducted repeatedly in terrestrial systems with mixed success (see Myers et al. 2000); equally, eradication and control of exotic seaweeds have been attempted in the past with similar, mixed results. Similar to the results of this study, attempted removal of *Sargassum* in areas in Europe proved unsuccessful (Gray and Jones 1977; Critchley et al. 1986). Attempted control of *Undaria pinnatifida* in Monterey harbor, California was also relatively unsuccessful (SIMoN website – sanctuarysimon.org). In Hawaii, where numerous non-native seaweeds are present, manual removal was largely unsuccessful due to the ability of non-native seaweeds to regrow from fragments (Smith et al. 2004; Conklin and Smith 2005). Alternatively, there has been moderate to high success in removal of other non-native seaweeds. Removal of floating mats of the brown alga *Ascophyllum nodosum* in San Francisco Bay, California occurred in 2002 and in 2008 to some success; the species has not been subsequently observed since the mats were removed, thus there was potential success in halting actual establishment (Miller et al. 2011). In San Diego, California, efforts to eradicate populations of the invasive green alga *Caulerpa taxifolia* were successful (Anderson 2005; Merkel and Associates, 2006). Here, $7 million was spent to remove *Caulerpa* through tarping the seaweed and pumping chlorine under the tarps. Early detection was crucial in leading to successful eradication in this case. Eradication of *Caulerpa taxifolia* in Australia through salt treatments revealed some success in localized areas but not in every location treated (Glasby et al. 2005). In New Zealand, the exotic kelp *Undaria pinnatifida* was removed mechanically, with additional trials of heat and chemical treatments to target microscopic gametophyte stage (Hunt et al. 2009; Forrest and Hopkins 2013). Here, sustained mechanical removal over a long period was successful (Forrest and Hopkins 2013) in reducing recovery except for locations where repeated introductions occurred (Hunt et al. 2009). The recovery of *Undaria* after removal in Tasmanian locations was suggested to be due to the need for repeated removal efforts as microscopic seed banks could persist for 2.5 years; these microscopic stages are extremely difficult to detect and remove (Hewitt et al. 2005).

In this study, removal was only conducted during a brief period at the beginning of the study. A possible strategy, if desired, could be a systematic and sustained eradication effort whereby non-native seaweeds are removed on a persistent basis. However, given the quick recovery, removal areas would likely need attention several times per year with high effort and costs required. Sustained removal has been linked to success in some studies (Forrest and Hopkins 2013) while lack of sustained removal has been linked to failures (e.g. SIMoN, Hewitt et al. 2005). The best approach is to look toward the future and increase efforts to prevent new introductions through increased monitoring. This would lead to early detection followed by a rapid response to eradicate or control the spread through a series of action plans prepared prior to detection (Lodge et al. 2006; Schaffelke et al. 2006; Williams and Smith 2007). It is clear that a rapid response was not undertaken with *Sargassum,* first detected in southern California in the 1970s, nor with *Caulacanthus*, first detected in 1999. Furthermore, the recent discovery of *Sargassum horneri* in 2003 in southern California waters (Miller et al. 2007) was also not acted upon; this species has now become widespread throughout much of southern California (Smith, pers. obs), including the subtidal habitat off Little Corona del Mar.

<u>*Sargassum muticum.*</u>

Sargassum muticum is a global invader, common throughout many parts of the world. In both the intertidal and subtidal habitats along the eastern North Pacific coastline, this species has become a major contributor to community composition since the 1970s. This ecological study of the impacts of *Sargassum* on native community structure and abiotic conditions in tidepools, feasibility of local eradication, and impacts of native herbivores reveals the follow highlights:

- The presence of *Sargassum* did not appear to have an impact on the abundances, diversity, or community structure of tidepool assemblages as tidepools with and without *Sargassum* were mostly similar.
- *Sargassum* did affect some abiotic characteristics of tidepools, such as causing a marked reduction in light penetration and a buffering of temperature changes during low tides.
- Removal of *Sargassum* from tidepools required a large amount of effort for a small spatial area with a more site-wide removal effort likely to be costly.
- Removal of *Sargassum* was ineffective as the seaweed recovered relatively quickly.
- Urchin herbivores may have a small impact on *Sargassum* abundance and recovery but are unlikely to provide control of the seaweed due to lack of herbivory because of high chemical defenses (phlorotannins) or because herbivory rates are lower than seaweed growth rates.
- Due to the lack of impact on native communities, the large effort required for removal, and lack of success of removal, it is believed that eradication efforts are not worthy.

The presence of *Sargassum* in intertidal tidepools in Newport Beach did not appear to have major repercussions on the abundances of native species nor on community assemblages. Wilson

(2001) found similar patterns across the California coast when comparing *Sargassum* pools with pools lacking *Sargassum* (either naturally or experimentally). However, in Washington State, *Sargassum* excluded many native species and reduced richness when *Sargassum* was abundant but actually increased diversity and facilitated native species when *Sargassum* was in low abundance (White and Shurin 2011). Comparatively, in subtidal habitats along the eastern Pacific coast, *Sargassum* has been shown to negatively affect community structure, including reducing the recruitment and density of kelps and other fleshy algae (Ambrose and Nelson 1982, de Wreede 1983, Britton-Simmons 2004). The mixed results between intertidal and subtidal systems may be attributable to multiple factors, including that intertidal systems tend to be more driven by disturbance thus differences are harder to detect (Wilson 2001). In addition, since *Sargassum* grows much larger in subtidal habitats, it may have a greater impact (Wilson 2001).

The mixed impacts of *Sargassum muticum* on community assemblages is not limited to the eastern Pacific coast as negative, neutral, and positive impacts were observed in invaded portions of Europe. Staehr et al. (2000) found marginal effects on richness and diversity of macroalgae but did find differences in community structure of macrophytes. In particular, declines were observed in thick and leathery algae. In Spain, Viejo (1997) also found reduced abundances of leathery and foliose algae in pools dominated by *Sargassum*. However, Viejo (1997) also suggests that the spatial patchiness of *Sargassum* may reduce the overall impact at local and larger geographic scales. Also in Spain, Sanchez et al. (2005) found declines in the dominant foliose red alga *Gelidium* but also observed an increase in species diversity. Reductions in slower growing leather and foliose algae, also observed in other studies (Engelen et al. 2003; Britton-Simmons 2004; Harries et al 2007b), are suggested to be attributed to a reduction in light; slower growers tend to be light limited (Viejo 1997; Sanchez et al. 2005). In comparison, crustose algae and calcareous species that do well under low light were often not affected by *Sargassum* presence. In France, *Sargassum muticum* was found not to directly compete with the eelgrass *Zostera marina* but it did interfere with regeneration of the eelgrass bed (den Hartog 1997). Comparisons of associated epifauna varied in differences between *Sargassum* and native algae communities in Portugal but, in general, did not appear to have a severe negative impact (Engelen et al. 2013). Minimal impacts were also observed in Spain (Olabarria et al. 2009). Alternatively, native pipefish were actually enhanced by the presence of *Sargassum muticum* in the North Sea (Polte and Buschbaum 2008) as were epiphytic communities in Spain, Denmark, and the North Sea (Sanchez et al. 2005; Buschbaum et al. 2006; Thomsen et al. 2006). Mobile marine invertebrates, such as amphipods and littorine snails, have also been shown to increase due to an increase in available habitat and *Sargassum's* complex structure (Giver 1999).

The lack of impact of *Sargassum* on the community structure of tidepools in Newport Beach was somewhat surprising given the large abiotic changes that *Sargassum* cause, which include a large reduction in light penetration and a buffering of temperature changes in tidepool waters during low tide periods. Other studies have also shown large decreases in light, reducing light penetration by 97% of that of surface light (Critchley et al 1990). Although only weak patterns of sediment accumulation were found in this study, other research has shown high sediment entrapment (Critchley 1983; Critchley et al 1990). Although not specifically studied, the canopy provided by *Sargassum* may also act as a refuge from predation as species can hide in the alga as well as providing additional space for species to live on (Norton and Benson 1983; Viejo 1999). It is possible that the negative impacts of blocking of light are balanced by the positive impacts of temperature buffering, refuge provision, and additional surface area for species to live on.

Although no impact was observed on native flora and fauna in this study, the meio- and epifaunal species living within the *Sargassum* canopy itself was not quantified. Had this community been examined, significant differences may have been observed. In other studies, comparisons of mobile epifauna on non-native *Sargassum* and native canopy formers found minimal differences (Norton and Benson 1983; Viejo 1999), except for a small number of fauna that had high host-plant specificity (Viejo 1999). In general, *Sargassum* was inhabited by epifauna probably due to: the use of *Sargassum* epiphytes as habitat or food, the similarities in characteristics between *Sargassum* and similar native canopy formers, and the use of *Sargassum* as a food source (Viejo 1999). Studies examining epifauna were done by comparing native and non-native canopy formers. In the tidepools in Newport Beach, other canopy forming species in the tidepools were mostly absent, with the exception of *Phyllospadix* which is not comparable since it is found in a much lower zone. Therefore, *Sargassum* may be providing a unique canopy that can be used by multiple epiphytes and epifauna that is otherwise absent in these pools. Further investigations are needed.

Experimental, localized eradication of *Sargassum* from tidepools in Newport Beach proved to be unsuccessful as *Sargassum* recovered quickly. It is difficult to determine whether recovery occurred because of regrowth from holdfast remains that were not entirely removed, the more likely scenario, or whether recovery occurred through recruitment of new germlings. It is clear that *Sargassum* can easily grow back from the smallest of holdfast tissue left behind (Fletcher and Fletcher 1975, pers. obs.). Despite robust efforts to remove the entire holdfast, it was nearly impossible to know whether all biomass was removed, even through the repeated scraping of the rock surface. There is no indication that *Sargassum* can disperse through vegetative fragmentation, thus branches or blades that fell off during removal were unlikely to lead to recovery. Recruitment could explain recovery but new recruits were not observed in either the *Sargassum* control plots nor the non-*Sargassum* control plots. The combined removal of *Sargassum* and transplanting of *Phyllospadix* showed promise in reducing the rate of *Sargassum* recovery, but the failure of *Phyllospadix* to survive transplanting in several experimental pools inhibited any strong patterns from being observed.

Similar to this study, the mechanical removal of *Sargassum* in Europe was largely unsuccessful (Gray and Jones 1977; Critchley et al. 1986). These investigators noted that, in some cases, mechanical removal failed to remove the holdfast allowing regrowth to occur, which often recovered in higher density because of creation of bare space during the removal process (Fletcher and Fletcher 1975). The removal process could also facilitate dispersal through release of drift fragments that could release germlings. The use of chemical biocides were considered in these studies but dismissed due to lack of a biocide specific to *Sargassum* and the likelihood of environmental damage with chemical use (Davison 1999).

The potential for biological control has been considered. Active feeding on *Sargassum* does occur by urchins, sea hares, and some gastropods (De Wreede 1983; Critchley et al. 1986; Pedersen et al 2005, Thomsen et al. 2006). Sjotun et al (2007) show that *Sargassum muticum* germlings are heavily grazed upon in Europe and may be a limiting factor for the spread of the alga. For adult *Sargassum* individuals, however, it is unlikely that feeding rates of herbivores are high enough to control it abundance. Furthermore, a number of other studies suggest that herbivores actively avoid the seaweed (Britton-Simmons 2004; Vogt 2010). This study found that urchins had no long term impact on *Sargassum*, despite there appearing to be a relationship between urchin densities and *Sargassum* in tidepools. The urchin experiment revealed some patterns initially but the patterns did not remain throughout the entire study. This may have been driven by the slow decline of urchins in treatment tidepools over time, likely due to emigration. Repeated transplanting of urchins could be examined to determine its efficacy in reduced *Sargassum* abundances. However, much like sustained removal efforts, sustained transplant efforts would need frequent attention and would require a high amount of effort and cost. Anecdotally, the herbivorous sea hare *Aplysia viccaria*, the larger of the two *Aplysia* species in intertidal systems in southern California, appeared to have a large impact on *Sargassum* in non-experimental tidepools. This species feeds rapidly and in large amounts, thus could provide some control. However, this species is also moderately mobile and uncommon, thus it would be difficult maintain populations of this species in a target area.

Sargassum muticum, similar to other Fucales, accumulate secondary metabolites, or phlorotannins, that may account for up to 30% of the dry weight of the alga (Targett et al. 1995). Phlorotannins are believed to be the primary chemical defense against herbivores (Norris and Fenical 1982, Hay and Fenical 1988, Van Alstyne 1988) and may be the reason why urchins in this study did not have an impact on *Sargassum* abundance. The phenolic content of Fucales, and other brown algae, are known to vary greatly among species but also greatly within a species depending on habitat, grazing, geographic location, salinity, season, temperature, and other driving factors (Pederson 1984; Hay and Fenical 1988, Targett et al. 1992, Steinberg 1995, Hay 1996, Pavia et al. 1997, Van Alstyne et al. 1999, Hemmi et al. 2004). For *Sargassum muticum*, phenolic concentrations measured in other studies also have varied greatly. Plouguerne et al. (2006) showed high temporal and spatial variation in France, with ranges from ~0.5% to 6.5% over time and across locations. Other studies report typical concentrations between 3.8-5.8% (Steinberg 1985, 1986; White 2003; Le Lann et al. 2008); the concentrations measured in southern California (5.1%) were within this typical range. There were no differences in phlorotannin concentrations among samples collected subtidally and from the high, middle, and lower intertidal zones. There were, however, differences in concentrations among the different species of *Sargassum* found in southern California. The native *Sargassum palmeri* contained only low levels of phlorotannins while the native *Sargassum agardhianum* contained similar levels to *Sargassum muticum*. The relatively newly introduced *Sargassum horneri* had the highest concentrations (7.2%)

The phlorotannin concentration of seaweeds can play a role in the frequency that the seaweed is grazed by herbivores. This is particularly important for exotic species that have been introduced into a new area. Exotic seaweed species that have a high phlorotannin concentration are released of herbivore stress and can therefore expend more energy on competition, growth, and reproduction and thus successfully establish and spread into a new area. Wikström et al. (2006) found that *Fucus evanescens* individuals that were introduced to Sweden had fewer herbivore species living on them than native species in Sweden. They also analyzed the native and non-native species in Sweden for phlorotannin concentrations and found that *F. evanescens* had higher phlorotannin concentrations than native species. The high phlorotannin concentrations that are found in the non-native *S. muticum* and *S. horneri* may be allowing these species to be successful in southern California.

<u>Caulacanthus ustulatus</u>

As with *Sargassum muticum*, *Caulacanthus ustulatus* is a major component of rocky intertidal shores in Newport Beach and other locations in the region. This study examining impacts on native assemblages and effectiveness of removal reveal the following highlights:

- *Caulacanthus* provides a novel turf in the upper intertidal zone, where macroalgae is uncommon in the region, which reduced macroinvertebrates and facilitated the presence of seaweeds and meiofauna that used the turf as refuge.
- *Caulacanthus* did not impact native communities in the middle intertidal zone where a native turf exists.
- Small scale removal experiments were unsuccessful, with regrowth occurring quite rapidly.
- A weak pattern of increased cover of *Caulacanthus* in removal plots suggests that removal may increase the presence of *Caulacanthus* by opening up new bare space.
- The effort required for *Caulacanthus* removal and low success suggest that larger scale eradication efforts are not feasible.

The presence of the non-native seaweed *Caulacanthus ustulatus* has resulted in significant alterations of the community composition of the upper rocky intertidal zone in

Newport Beach, California; a similar pattern was also observed at other sites in the region in a similar study conducted in 2011 (Smith, unpublished data). Non-native *Caulacanthus* patches tend to have a weak pattern of lower diversity of macroinvertebrates, with a decrease in the abundance of barnacles, limpets, and periwinkle snails. *Caulacanthus* growing in the upper intertidal zone can inhabit space normally used by barnacles and limpets with the alga observed growing over and possibly smothering barnacles and inhibiting filter feeding. On multiple occasions, dead barnacle tests were observed within the turf. Upper intertidal zone patches dominated by *Caulacanthus* also contain a different and more diverse assemblage of seaweeds with *Caulacanthus* patches having more fleshy seaweeds, while native patches have few seaweeds, dominated by the encrusting variety. The subplot sampling, intended to target meiofaunal assemblages, also differed markedly with native patches dominated by adult and juvenile barnacles and limpets while the non-native patches contained a higher variety of turf inhabiting meiofauna. The patterns observed suggest that the novel turf that *Caulacanthus* forms in the upper intertidal zone, where native turfs are rare in this region, creates a refuge for seaweeds and meiofauna to inhabit. Turf forming algae, such as *Caulacanthus*, have a high water-holding capacity during low tide (Hay 1981), which may decrease desiccation stress allowing seaweeds and other organisms inhabiting the turf to thrive in the upper intertidal zone where they normally cannot exist. In addition to reducing desiccation stress, *Caulacanthus* turfs trap sediment and small debris that is otherwise absent in native patches, which can provide food and habitat for turf inhabiting meiofauna. Although some meiofauna can partially depend on barnacle test presence, many meiofauna are benefitted by the presence of turf forming algae that increases habitat complexity (Hicks 1980; Gibbons and Griffiths 1986; Gibbons 1988). Comparisons of meiofauna along a gradient of intertidal microhabitats (barnacles, rock, turfs, fleshy seaweeds) reveal peak densities within algal turfs, particularly when sediment is trapped in the turf (Gibbons and Griffiths 1986); increases in nematodes, foraminifera, and copepods were also found to be correlated with sand and algal turf, rather than algal biomass (Gibbons and Griffiths 1986). Additionally, meiofaunal ostracods have been shown to be more abundant and diverse in turf assemblages, likely due to the heterogeneity of the turf algae habitat and accumulation of sediment (Frame et al. 2007). Meiofauna can also obtain refuge from predators in turf forming algae (Coull and Wells 1983) as the turfs provide an increase in habitat complexity reducing predator capture rates.

To examine the novel turf forming hypothesis of *Caulacanthus* in the upper intertidal zone, community assemblages in native and non-native patches in the middle intertidal zone where a native turf naturally exists were also examined. The middle intertidal zone of southern California is dominated by turf forming algae, consisting primarily of articulated corallines (e.g. *Corallina*), small red algae (e.g. *Chondracanthus*, *Gelidium*), and filamentous-like algae (e.g. *Ceramium*, *Polysiphonia*, *Centrocerus*, *Cladophora*); *Caulacanthus* is typically growing within this turf, rarely observed growing on its own. Community composition, in general, was similar in middle intertidal native and non-native turf patches suggesting *Caulacanthus* is not impacting native assemblages in this zone. This is likely because a native turf is already established and that *Caulacanthus* is not providing a novel habitat-type within the middle intertidal zone as it does in the upper intertidal zone.

The localized eradication of *Caulacanthus* was unsuccessful as the seaweed grew back quickly. Recovery can be attributed to several possible reasons: 1) the regrowth of *Caulacanthus* from prostrate crusts that were missed during the removal treatments, 2) the survival of crust portions of the alga from scraping and torching, 3) the recruitment of new individuals from sources outside of the treatment plots, or 4) the growth of *Caulacanthus* from outside of the plot into removal areas. More than likely, recruitment was not a major driver but it is hypothesized that the remaining scenarios all played an important role. It is feasible that some portions of the prostrate crust portion of the seaweed were missed during removal treatments as there were many cracks and crevices in the rocks were the alga may have found refuge. However, with use of a propane torch (specifically to target cracks and crevices where scraping would not be effective) to burn all materials in the rock, it seems that a very large portion of live algae, even in cracks and crevices, were heated to temperatures that would kill the alga. Therefore, missed materials would be limited in nature and not, observationally, reflective of the high amount of recovery. Despite being counterintuitive, it is believed that some crust portions of the alga survived the torching process. This is evident when looking at patch growth patterns within the plot whereby the same growth pattern was observed prior to torching and after recovery (e.g. Figure 44). Qualitatively, it also appears that *Caulacanthus* displays a unique growth and spread pattern. In essence, this seaweed seems to move around the rock as it creepily grows along the substrate, receding and advancing in multiple directions, sometimes dying in older growth areas. On several occasions, *Caulacanthus* cover was highly variable within a plot, including non-

Caulacanthus control plots, which anecdotally, are attributed to the ebbing and flowing of new growth. Even with the scraping and torching of a buffer around treatment plots, there were cases were growth moved in from surrounding rock habitat. If the unique spread of this species is valid, a possible approach to minimize recovery would be a full scale removal at a site. As mentioned, however, this is likely a large, costly effort that would also lead to the destruction of native species during scraping and torching. In addition, if survival of the crustal portions is true, there would likely be a failure in full scale removal. Although a weak pattern, it is also suggested that scraping and torching opens up new space which leads to a higher recovery of *Caulacanthus* as no other species are inhabiting that space.

The addition of limpets as a means to control *Caulacanthus* recovery also failed. While it is known that the limpet *Lottia scabra* is not a macroalgal grazer, it does scrape the rock using its radula in search of microalgae. Microalgal grazers are known to also remove and/or consume the microscopic stages of macroalgae and, possibly the crust stages (Branch 1981; Morelissen and Harley 2007). In the high intertidal zone in Newport Beach, and in southern California, there are few macroalgal grazers present, thus *L. scabra* was the best possible choice. In addition to there being a lack of upper intertidal macroalgal grazers, there are few grazers in general that are adapted to consume red algae which are typically heavily chemically defended. While the chemical defenses of *Caulacanthus* are unknown, the lack of feeding on this alga by dominant macroalgal grazers in the region (Navarro 2009; Vogt 2010), except *Aplysia californica* which is known to target red algae with high chemical defenses, suggests they do contain these secondary metabolites. The lack of success of limpets to control recovery may be due to its inability to consume red algae, even the microscopic or crust stages. Additionally, regrowth may have occurred at faster rates than the limpets could consume. This may have been a reason for the decline in limpets in transplant plots towards the end of the experiment as limpets were being crowded out. However, given the low amount of *Caulacanthus* in the plots towards the end of the experiment, this is unlikely. Equally, the large decline in *Caulacanthus* cover in unmanipulated control plots may have limited the ability to detect limpet impacts.

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